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Deer browsing on Norway spruce in relation to supplemental feeding –not a matter of distance only

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Abstract

The causes of the browsing intensity are not fully understood and even less for this non-preferred and economically valuable tree species. Browsing pressure on spruce trees (*Picea abies*) caused by fallow deer (*Dama dama*) around supplemental feeding sites was investigated. Trees were classified in three different categories to cover the variability in height i.e. trees < 1m, 1-4m and > 4m. The study was performed in southwestern Sweden, within an estate with an artificially maintained high deer density. I quantified the browsing pressure on spruce and investigated which factors had a significant effect on the found browsing pattern in relation to supplemental feeding sites.

A total of 25.7% of the surveyed trees were affected by browsing, being the smaller category the less consumed probably due to a higher content of secondary metabolites. Using model selection procedures the factor browsing pressure on pine appeared as the most important explaining up to 40% of the response variability. Other important factors were the distance from the feeding sites, the shape of the spruce trees and the structural complexity (multi-layered forest stand). However not all the important factors had the same effect in relation to the different response variables. Deciduous tree density and amount of shrub species did not exert a significant effect on browsing. These high browsing values on spruce were caused by the attraction exerted by the supplemental feeding sites and the high density of herbivores maintained, even though artificial food was supplemented *ad libitum*.

Key words: Browsing pressure, Dama dama, deer density, spruce, Picea abies, artificial feeding stations, silage.

Contents

Introduction

Ungulates are important for ecosystem functioning and their importance as ecosystem drivers are apparent especially when main predator species are absent. The successful recovery of ungulate populations during the past 50 years, has led to an increasing number of high density deer populations for which ultimately, management is necessary (Danell et al. 2006). Irrespective of whether the management goal or strategy is focused on a certain game species, biodiversity issues, or protection of valuable forest plantations, it is of paramount importance to understand the target species foraging pattern and resource utilization (Gordon 1989), to infer their effect on ecosystems (Senft et al. 1987, Augustine & McNaughton 1998, Coulson 1999, Reimoser 2003, Côte et al. 2004, Danell et al. 2006).

At the landscape scale is the available forage occurring in variable quality and quantity, determined by seasonal and even daily changes, for which herbivores adapt their spatial foraging strategy accordingly (Moen et al. 1997, Côte et al. 2004, Newman 2007). Increased forage availability at certain areas can attract browsers but at the same time it can also decrease total damage level at large scale, given a constant herbivore density (Gundersen et al. 2004). It has also been demonstrated the relation between deer density and forest damage. They are positively correlated increasing the level of damage as deer density increases (for review see Gill 1992), although it is known that the vegetation functional response to browsing is not linear, which suggests a careful research (Gill 1992b). Intense browsing by deer is widely considered as a problem in forest regeneration (Bergqvist et al. 2003) and limits tree growth and survival, reducing also timber quality (Welch et al. 1992; Gill 1992).

Supplemental feeding and browsing pressure

Supplementary winter feeding of large ungulates is a common practice throughout northern Europe and parts of North America (Putman & Staines 2004). According to Voigt (1990) and Doenier et al. (1997), supplemental feeding involves feeding deer to augment forage regardless of winter conditions, which consequently can have an effect on how deer impact their habitat (Doenier et al. 1997). Indeed, foraging patterns and animal behaviour and distribution, is affected by resource availability and distribution in

the landscape (Sahlsten et al. 2010). These changes of foraging patterns promoted by changes in forage availability have been observed for red deer *Cervus elaphus* (Smith 2001), white-tailed deer *Odocoileus virginianus* (Doenier et al. 1997; Cooper & Owens 2006), roe deer *Capreolus capreolus* (Guillet et al. 1996) and moose *Alces alces* (Gundersen et al. 2004). The rationale behind supplemental feeding is usually associated with the maintenance of animals at high densities for hunting, and the prevention of possible forest and agricultural damages, among others (Peek et al. 2002; Putman & Staines 2004), whose effectiveness is, in turn, still unclear (Putman & Staines 2004).

The use of supplemental feeding as a countermeasure to prevent damage on vulnerable trees or agricultural crops is equivocal, although, in several studies has the management action successfully been tested (Steinn 1970; Long 1989; Ball et al. 2000; Peek et al. 2002; Sahlsten et al. 2010). In contrast, browsing pressure or damage has been shown to increase locally around supplemental feeding sites in response to the increased density of animals (e.g. Schmidt & Grossow 1991; Hörnberg 2001; Gundersen et al. 2004). In this light, Sahlsten et al. (2010) determined that the increment of areal use of moose in the near vicinity of the supplemental feeding sites reaches a distance up to 100-200 m.

There are three main causes of tree damage by deer. They can be due to browsing, stripping bark and by fraying trees with antlers (Gill 1992). Deer feeding adaptations are classified within a range from true highly selective browsers to mixed feeders with a high content of grass in the diet, some showing preferences for certain plant species, and consequently, the effect of browsing to the habitat not only depends on plant palatability, availability and composition but also on deer species (Gill 1992). Conifers are usually browsed in winter, whereas broadleaves are commonly consumed in summer (Miller et al. 1982; Klein et al. 1989; Maizaret & Ballon 1990), with some exceptions such as willow *Salix* sp. that contribute significantly to red deer and roe deer winter diet (Szmidt 1975; Jamrozy 1980). Browsing may halt tree growth for several years or decades (Roth 1996; Bergquist et al. 2003). For example, in a simulated browsing experiment on Norway spruce (*Picea abies*) height growth reduction was linearly correlated with the number of years the browsing experiment was applied (Mitscherlich & Weise 1982).

Moreover, browsing pressure can be influenced by the relative palatability of the species (Gill 1992), i.e. tree species are not proportionally used to their availability (Månsson 2007). Consequently, tree species can be ranked according to their relative preference, establishing rowan (*Sorbus aucuparia*) as the most preferred and Norway spruce as the least prefered (Bergström & Hjeljord 1987). Eiberle and Bucher (1989) exemplified this concept when browsing by roe deer on silver fir (*Abies alba*) was studied. They found a reduction in browsing when the surveyed species was associated with more palatable ones like ash (*Fraxinus excelsior*), rowan and sycamore (*Acer pseudoplatanus*), but the opposite effect when less palatable species were abundant like beech (*Fagus sylvatica*) and Norway spruce.

Alternative food sources have also been suggested to have an opposing effect on browsing damage (Mitchell & McCowan 1986). This was also shown by Welch et al. (1991), where browsing caused by red and roe deer on Sitka spruce (*Picea sitchensis*) in winter was mainly associated with ericoid shrub cover.

Aim

In this study I investigate deer browsing pressure on the predominant and economically most important tree species in the study area (Norway spruce), in relation to supplemental feeding sites. Since spruce is the dominant but also one of the least preferred tree species, it is assumed to be a subtle indicator of deer browsing pressure and its spatial distribution around the artificial feeding sites. By determining the spatial pattern of the browsing pressure it will also be possible to elucidate which are the key factors of the habitat, significantly related with browsing. More specifically, the research questions and hypothesis tested are:

- Quantifying the browsing pressure on Norway spruce in three height classes i.e. (1) < 1 m; (2) 1 - 4 m and (3) > 4 m. A higher occurrence of browsing in smaller trees was hypothesized since the most vulnerable height range is suggested to be between 30 – 60 cm (Staines and Welch 1984; Welch et al. 1988, 1991 in Gill 1992). The first and second height classes are the ones that if browsed, will suffer the largest growth reduction and morphological alterations, which in turn will affect future economic value (Gill 1992; Welch et al. 1992).

- Investigating how the browsing pressure is related to distance to supplemental feeding sites. Browsing pressure is expected to decline with distance from supplemental feeding sites (decreasing the proportion of twigs browsed as distance from supplemental feeding sites increase) as central place foraging theory suggests (Schoener 1979; Rosenberg & McKelvey 1999).

- Elucidating the factors that may have a significant effect on the found browsing pattern on Norway spruce.
    - The following factors will be tested: Dominating forest type, Structural complexity (multi-layered forest stand), browsing pressure on pine, alternative food (amount of shrubs species such as blueberry (*Vaccinium myrtillus*), lingonberry (*V. uliginosum*) and heather (*Calluna vulgaris*) present) and Deciduous tree density.

- Investigate the effect of the type of supplemental feeding site for the browsing pattern. Half of the stations surveyed provide supplemental food for both fallow deer and wild boar, while the other half provide food for fallow deer only, consequently the potential areal interference of both sympatric species will be tested.

- The effect of tree morphology on browsing pressure. Norway spruce is one of the least preferred species but still browsed, could the trees selected for browsing be based on tree morphology?

Methods

Study area

The study was performed at the Koberg estate (latitude 58°N & longitude 12°E), within Västra Götaland County in south western Sweden (Fig. 1). The area is approximately 90 km^2 in which *ca*. 79 % consists of forested areas, 16% arable land and pastures, and 5% consist of mires, marshes, lakes and parks (Winsa 2008) (Appendix I). The open arable land and pasture are cultivated to enhance the carrying capacity of the habitat, to sustain higher densities of large herbivores. Deer population is artificially fed *ad libitum* with a total of 500-700 tons/year of silage.

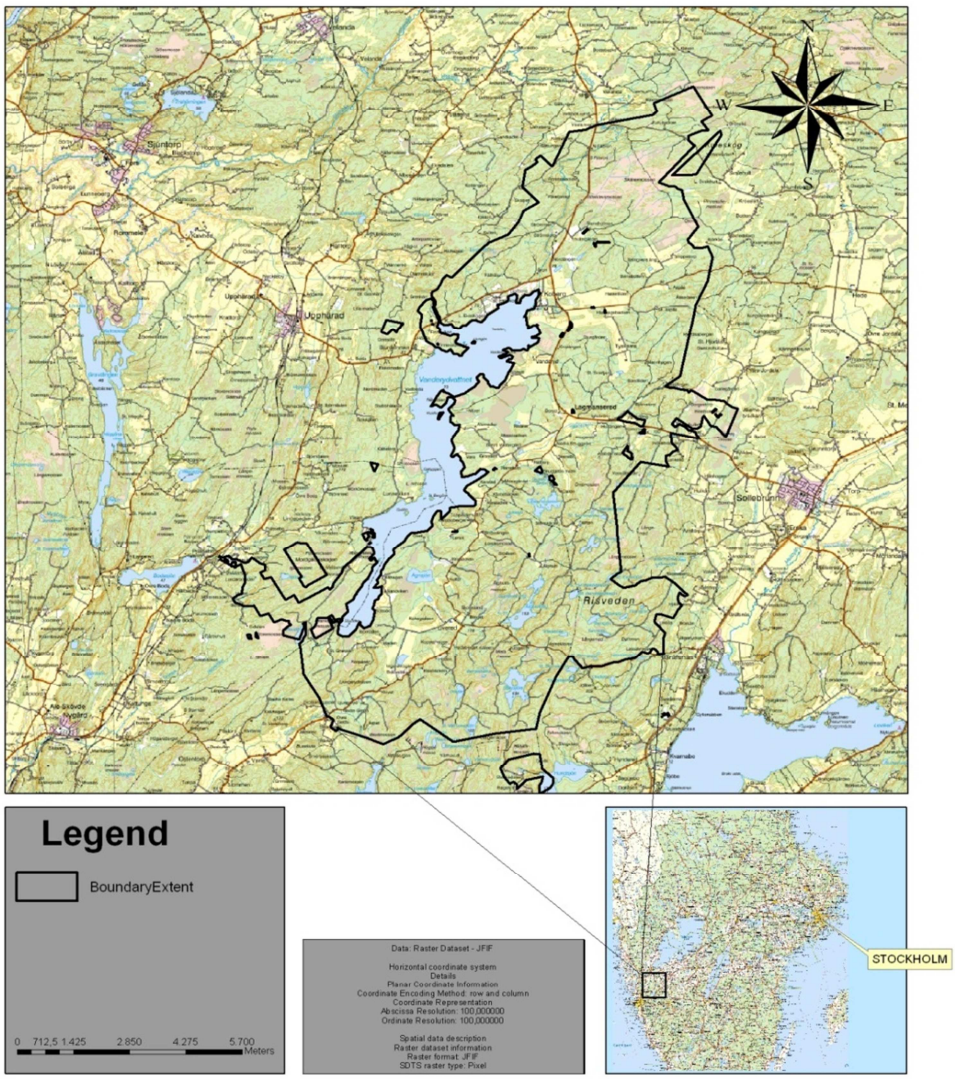


Figure 1. The 10 000 ha study area indicated with a black boundary in the top panel, and its location in south western Sweden (bottom right panel).

Fallow deer and other ungulates in the study area

The European fallow deer was introduced in Sweden *ca*. 1570's (Carlström & Nyman 2005). Presumably due to herd characteristics and the capacity of adaptation to different environmental conditions, its use as a game species was initially promoted at the estates and among noble Swedish families. Nowadays, fallow deer has viable populations up to latitude 64ºN being present in wild conditions in all except one (out of 21) Swedish provinces (P. Kjellander, unpubl. data) with an annual reported harvest of 20 000 individuals (Jägareförbundet 2011).

At the study area (Koberg Estate), approximately 20 fallow deer were introduced in the 1920's. In April 2007, the free ranging fallow deer populating the estate was estimated to 2600 individuals (327 animal/1000ha) by the "Distance sampling" method (Buckland et al. 2001; P. Kjellander, unpubl. data). This high deer density has during the past 10 years been maintained by supplemental food provided *ad libitum* during 3-4 winter months. In total more than 50 supplemental feeding sites are distributed throughout the 10.000 ha large estate. Several of these feeding sites also provide supplemental forage all year around for wild boar (*Sus scrofa*). Apart from wild boar and fallow deer there are also roe deer and moose present in the area with densities of 17 and 6.5 animal/1000ha, respectively (P. Kjellander, unpubl. data).

Study design

A total of 24 supplemental feeding sites were selected to measure the herbivore browsing pressure upon conifer tree species, especially focusing on Norway spruce. The target feeding sites were selected based on its location i.e. the selection was made to cover homogenously the whole study area. The balance among feeding site type was kept selecting half exclusively designed for deer and the other half for wild boar and deer. This made possible to test whether it existed a significant interference in the use of the feeding sites by both sympatric species related with browsing behaviour. However, the other existent supplemental feeding sites could have an effect in the results, although in the field none overlap between the surveyed transects and the non-selected feeding sites was observed. The sample size as a consequence is assumed to be representative of the reality observed.

For each station and in each cardinal direction, six plots were surveyed at 0, 50, 100, 200, 300 and 400 m distance (Fig. 2) from the artificial feeding sites (summing a total of 557 surveyed plots). Plot 0 was always defined as the closest conifer tree to the centre in the surveyed direction. The first three plots were separated with only 50 m to increase the resolution in the first hundred meters, and the maximum length (400 m) was set, according to the distance in which the use of supplemental feeding sites by moose declines (Sahlsten et al. 2010). Once the plot 0 was defined, a 400 m long transect was designed using a hand held GPS (GPSMAP 60CSx; Garmin international Inc.), along with the rest of the plots at fixed distances. When encountering non-forested areas, all plots were moved until the next forested area was reached, or until a maximum transect length of 500 m. Otherwise the survey was shortened.

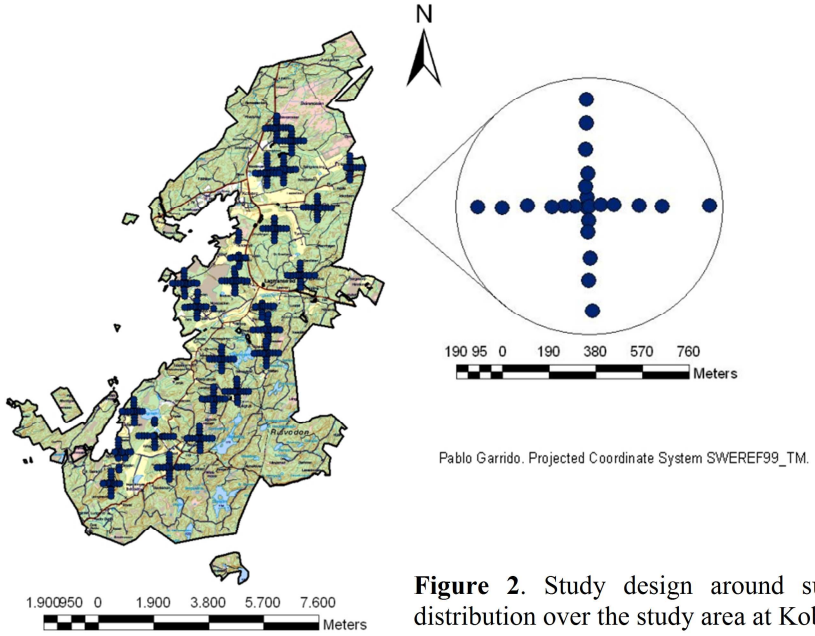


Figure 2. Study design around supplemental feeding sites and distribution over the study area at Koberg in south western Sweden.

Vegetation surveys

Conifer tree species

Scots pine (*Pinus sylvestris*) and Norway spruce were classified into three different height classes in order to cover the tree height spectrum in the study area: (1) < 1 m, (2) 1 – 4 m and (3) > 4 m. From the center of each plot within a 4 m radius, up to six target trees were selected (one per class and species). The closest trees to the center of the plot were measured. To estimate browsing pressure on spruce two branches per tree were selected at random for detailed inspection. The branches were chosen within a height

range of 0.5 to 2 meters at the target trees. They were visually classified in one out of 5 categories (Appendix II). The Class 0 was defined as trees without branches, with dead branches, dried or not available; for categories 1, 2, 3 and 4, a five branch sample for each category was taken and the total number of twigs accessible for the herbivore fauna counted and averaged (Appendix II). The selection of the branch samples was based on the different number of twigs per branch (twig density per branch) observed in the field. The number of twigs per category was estimated at 127, for the first category; 293.2, for the second; 515, for the third and 876.4, for the fourth category. The diameter of the stems was measured with caliper (note: the diameter was measured at diameter at breast height: 1.3 m (DBH), unless trees were less than 3 meters high, taken the measurement at ground level) and height estimated by visual comparison with a two meter stick (Appendix III).

Moreover, when small selected trees and branches contained less than one hundred twigs, all their twigs were counted instead of classified into the mentioned categories. All browsed twigs per branch were counted and a sub-sample of five browsed twigs selected to measure the twig diameter from the bite. This twig diameter was measured with a precision caliper in millimeters.

Deciduous tree species

Due to the scarce occurrence of deciduous trees, a continuous 400 x 2 m line transect was performed. Start and end points of each transect were defined in accordance with the previous plots defined at the conifer survey i.e. the transect started in the center of plot 0 and ended in the center of the plot 400 for each cardinal direction. When plots of the conifer survey were moved to avoid non-forested areas (crops, fields, lakes etc.), the deciduous survey was modified accordingly. All the deciduous trees within the transect (direction) were counted (Appendix IV). Thus an estimation of the deciduous trees density was obtained (the same deciduous tree density was assumed for all plots in each direction). This was done to elucidate whether alternative food positively or negatively affect the browsing pressure on spruce. Only the main species were surveyed i.e. the ones with higher probability of occurrence in the study area, within six categories (5 defined tree species and one group of rare species). In a decreasing scale of occurrence,

the following are: silver birch (*Betula pendula*), downy birch (*Betula pubescens*), willow (*Salix* ssp.), pedunculate oak (*Quercus robur*), aspen (*Populus tremula*) and the class others that comprises: small-leaved lime (*Tilia cordata*), ash (*Fraxinus excelsior*), Scots elm (*Ulmus glabra*), Norway maple (*Acer platanoides*) and rowan (*Sorbus aucuparia*).

Field layer (shrub species)

The available biomass of five different shrub species was surveyed (blue berry (*Vaccinum myrtillus*), lingon berry (*V. vitis-idea*), bog-blue berry (*V. uliginosum*), heather (*Calluna vulgaris*) and bramble[1] (*Rubus* ssp). In the center of each plot, a 25x25 cm wooden frame was placed and all living plants of the 5 target species were cut with a scissor, separated in different paper bags and dried at 70º Celsius for minimum of 72 hrs. The dry matter was weighted to the near centigram with a precision scale. Both bog-blue berry and bramble were finally disregarded due to their scarce occurrence.

Habitat description

A habitat description for each plot was performed by visual estimation of the presence of tree species (%) (spruce, pine, birch, aspen, rowan, oak and willow) within a 10 m radius. Moreover, the stand status was also estimated, distinguishing between clear-cut, plantation (< 1 m), young (1.1 - 2 m), young (pre-commercial thinning) (2.1 – 5 m), thinning (5.1 – 15 m) and old growth (> 15 m) (Appendix III).

[1] Bramble is expected to be found with difficulties due to its highly preference by large herbivore fauna, and the habitat characteristics in the study area (mainly according to the disturbance regimes), which are not the optimal for the occurrence of the species.

Preliminary variables for modelling

Response variables

Browsing pressure

The term "browsing pressure" is defined as the proportion of browsed twigs (shoots) per selected branch category at the target trees during the previous winter (see vegetation survey on conifer trees). However, with the present study design it was not possible to distinguish among the different species of browsers populating the study area. Thus, it is assumed that browsing pressure is mainly exerted by the abundant fallow deer population, which comprises more than 93% of the herbivores coexisting at the study area. In contrast, this assumption it can also affect the results obtained. In the present study, only browsing pressure on spruce is used as a response variable. It was also separated in three classes or categories, related to tree height:

y1➔ Browsing proportion in spruce less than 1 meter high (0 to 1).
y2➔ Browsing proportion in spruce 1 to 4 meters high (0 to 1).
y3➔ Browsing proportion in spruce more than 4 meters high (0 to 1) .

Predictors or explanatory variables

Deer station (DS): Dummy variable (0 or 1), acquiring the unit value when the feeding site is designed just for deer (silage only) and zero when designed for wild boar and deer (silage and corn).

Direction (D): Categorical variable constituted by the four transect directions: North, East, West and South.

Distance from supplemental feeding site (Pt): Treated as a continuous variable. Represents the distance to the center of the supplemental feeding site at 0, 50, 100, 200, 300 and 400 meters, in which the response variable was measured.

Shape of spruce categories 1,2 & 3 (S1;2;3): The variable shape of spruce trees was created for each of the three tree height classes. The shape index was constructed as a ratio between diameter and height [cm/m].

Shape of pine categories 1,2 & 3 (Sp1;2;3): The variable shape of pine trees was created for each of the three tree height classes. The shape index was constructed as a ratio between diameter and height [cm/m].

Browsing pressure on pine categories 1,2 & 3 (Bp1;2;3): Browsing pressure on pine was created for each of the three tree height classes, as the proportion of browsed twigs previously defined (see *Response variables*).

Shrub species (BLH): Quantitative variable in [g/m^2] estimated by the sum of available dry biomass of blue berry, lingon berry and heather sampled at each plot (the other two species were excluded due to their scarce occurrence).

Deciduous tree density (TD): Continuous and quantitative variable [$trees/m^2$], that represents the density of deciduous tree species along the surveyed transect**.**

Structural complexity (SC): Describes the structural complexity of the plot (i.e. multi-layered tree stand). A categorical variable that represents the distinct forest stand management stages (silvicultural stages), that can be found in the surveyed plots, i.e. plantation (< 1 m), young (1.1 – 2 m), young (pre-commercial thinning) (2.1 – 5 m), thinning (5.1 – 15 m) and old growth (> 15 m), in a range of 1 to 5.

Forest type (FT): Forest type was calculated using the percentages of the main tree species surveyed at each plot. This variable represents the main tree species composition of the forest stand. The classification was made according to Riksskogstaxeringen (2006) standards as follows:

- Spruce forest: Containing ≥ 70% spruce trees species at the plot.
- Pine forest: Containing ≥ 70% pine trees species.
- Mixed coniferous forest: Containing ≥ 70% coniferous tree species.
- Mixed deciduous forest: Composed by 31 to 69% of deciduous tree species.
- Deciduous forest: Containing ≥ 70% deciduous tree species or ≥ 50% of hard wood tree species such as pedunculate oak (*Quercus robur*), European beech

(*Fagus sylvatica*), elm (*Ulmus ssp.*), ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*) etc.

Statistics and Modelling

Data exploration

Data exploration is a crucial part that should precede the statistical analysis, and most statistical violations can be avoided by applying a better data exploration (Zuur et al. 2010). Thus, type I and type II errors (type I error: rejecting the null hypothesis when it is true; type II error: failure to reject the null hypothesis when it is untrue), can be reduced or avoided, thereby minimizing the risk of making wrong ecological conclusions (Zuur et al. 2010).

The exploration is started by looking for outliers in variables with a high degree of heterogeneity. These specific values named outliers may cause overdispersion problems in General linear modeling (GLM) using Poisson or binomial distributions when in fact the result is not binary (Hilbe 2007). A common graphical tool used for outlier detection is the boxplot in which any data points beyond a certain limit are considered as outliers. Likewise, another graphical method to visualize them was utilized, which provides more detailed information than the boxplot, named Cleveland dotplot (Cleveland 1993). Thus, outliers were checked both in the response variable and in the predictor browsing pressure on pine (Appendix V).

Before including interaction terms in the models, it is essential to know whether the data is balanced or not. In this case, the data was too unbalanced therefore it was not possible to include any interaction terms, in order to reduce the probability of producing outcomes determined by a small number of influential observations (Zuur et al. 2010).

Variable selection procedure

To investigate the possible relationship of each explanatory variable with the response a one factor model for each predictor were constructed. However, the usual 5% significance level is too severe for model building purposes; therefore, a value less than 25% (McCullagh & Nelder 1989; Hosmer & Lemeshow 2000) was applied. Accordingly, only those significant enough to be included in the maximal model were

selected, for each of the three response variables (y1, y2 and y3). When a candidate predictor variable was not possible to include in the maximal model (e.g. due to excessive missing data, skewness of the whole model if included etc.), the one factor model for that candidate predictor was used to investigate the relationship. Another important question is to determine possible collinearity problems between covariates, which can led to type II errors. Consequently, correlation levels between the factors potentially included in the model was tested (Appendix V), in order to avoid the inclusion of strongly correlated variables (correlation coefficient > 0.5) in the same model (Edge et al. 1987).

Model selection

The approach was to work with GLM's, in which it is necessary to specify the distribution of the data, the link function which describes the relationship between the mean value and the variance in the distribution (see Olsson 2002), and the linear predictor. The choice of distribution affects the assumptions since the relation between the variance and the mean is known for many distributions (Olsson 2002).

In this case, since the response variable was a proportion (i.e proportion of browsed twigs) a Binomial distribution with a logit link was first tested. Due to the nature of the data set with many zero observations, the model using binomial errors did not fit adequately, leading to overdispersion. Thus, a quasi-binomial distribution was used specifying a more appropriate variance function, where the dispersion parameter is not fixed (Appendix VI). One disadvantage of the method is that it is not computing AIC (Akaike Information Criterion; Akaike 1974) values, because the log-likelihood parameter cannot be calculate, so the subsequent model selection procedure was limited. Another limitation is the impossibility to obtain the coefficient of determination, which expresses the amount of variation in the response variable that is explained by the model. The dataset was in this perspective too small and a major limitation for a successful analysis applying the above mentioned method i.e. too many cases with missing values. In consequence, I opted for finding the best transformation of the response variable to allow for a normal linear regression model to fit the data, previously tested lack of normality in the response variables by Shapiro-Wilk normality

test. Browsing data is commonly highly skewed, therefore, a log(x+1) transformation is suggested to normalize it (Krebs 1994).

A good model is a compromise between parsimony and completeness (Olsson 2002), and therefore the maximal model was fitted and five different model selection procedures were run to produce a group of parsimonious candidate models for each response variable (Appendix VII). The following model selection procedures were applied, using R 2.13.2 (R Development Core Team 2011) and the wle (Weighted Likelihood Estimation) package (Agostinelli 2010):

- Parsimony method: The parsimony principles (Occam`s Razor) for the simplification of the maximal model were used. Hence, all non-significant factors were removed until the group of models was obtained (one per response variable) (see Crawley 2005).

  The selection of an appropriate subset of explanatory variables is crucial in statistical analysis when linear regression models are used (Agostinelli 2002). However, classical stepwise regression methods can be invalidated by a few outlying observations (Agostinelli 1999; 2002). Here, based on data exploration it was assessed not to apply robust stepwise regression methods (Markatou et al. 1995; 1998).

- Mallows Cp: Mallows Cp is a method for model selection which uses the least square method to assess the fit of a regression model. It is applied when the objective is to select among a number of predictor variables to find the best model involving a subset of the latter (Mallows 1973). This method evaluates the Mallows Cp for each linear candidate model.

- Cross Validation: The Cross Validation method (Shao 1993) is used to choose a subset of the best linear candidate models. It selects a model with the best average predictive ability calculated based on all different ways of data splitting (Shao 1993). Hence, a group of parsimonious models for each response variable was obtained.

- Stepwise method: This procedure selects the best candidate model, using the least square method (Goldberger 1961). Thus, the best candidate model for each response variable according to this methodology was procured.

- Akaike Information Criterion (AIC): The AIC method (Akaike 1974; Shibata 1981) produces a set of candidate models based on the maximum likelihood principle. This method is discarding the variables that according to each AIC values are not adequate to form the parsimonious model.

This procedure resulted in a set of five potential best parsimonious models for each response variable. The parsimonious models were fitted and its diagnostic graphs plotted. In order to determine the best model among the candidates, three different criteria were used: the model significance looking at P value, the adjusted coefficient of determination, and the diagnostic graphs i.e. Residuals vs Fitted values, Standardized residuals vs Theoretical Quantiles (Normal Q-Q), Scale-Location (Standardized residuals square rooted vs Fitted values) and Residuals vs Leverage.

Different diagnostic tools have been developed but in the present study, the use of graphical tools was investigated as suggested by Montgomery & Peck (1992), Draper & Smith (1998) and Quinn & Keough (2002).

The classical application of linear models rest on certain sets of assumptions (Olsson 2002):

- The model used for the analysis is assumed to be linear and correct.
- The residuals (e_i) are assumed to be independent.
- The residuals (e_i) are assumed to follow a Normal distribution with mean zero.
- The residuals (e_i) are assumed to be homoscedastic i.e. to have a constant variance σ^2_e for all predictors.

Thus, graphical tools have been used to detect departures from these assumptions, however, only the failure on the Normality and Linearity assumptions can cause the model rejection.

Results

Descriptive statistics

Within a total of 557 surveyed plots, 723 spruce trees were measured (Tab. 1).

Table 1. Distribution of the surveyed trees in relation to each fixed distance from the supplemental feeding sites and in relation to tree category.

Number of target trees measured at fixed plot distance						
Response variables	Distance from supplemental feeding sites (m)					
	0	**50**	**100**	**200**	**300**	**400**
y1	35	48	45	44	38	39
y2	33	34	37	27	38	17
y3	45	51	46	44	49	53

From the first height category (i.e. < 1 m), 249 target trees were measured. In 308 plots this height class was not found. In total 20.5% of surveyed target trees were browsed. The mean browsing proportion per tree was 7.7±4.4% (mean±SD), and the mean diameter of the browsed twigs was 1.7±0.5 mm (mean±SD).

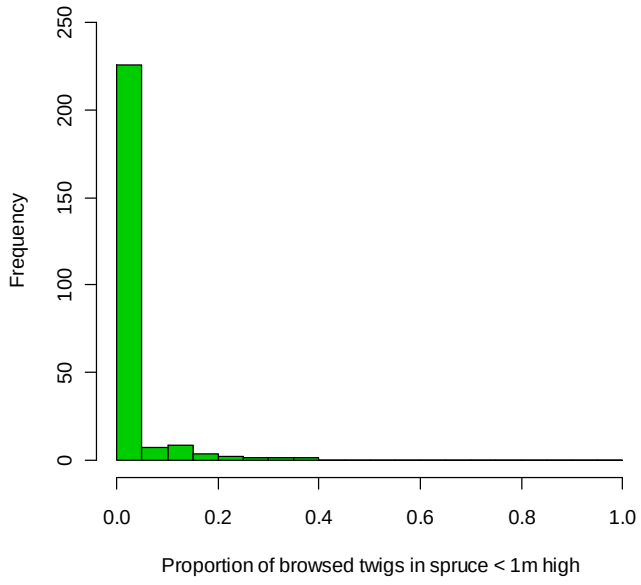
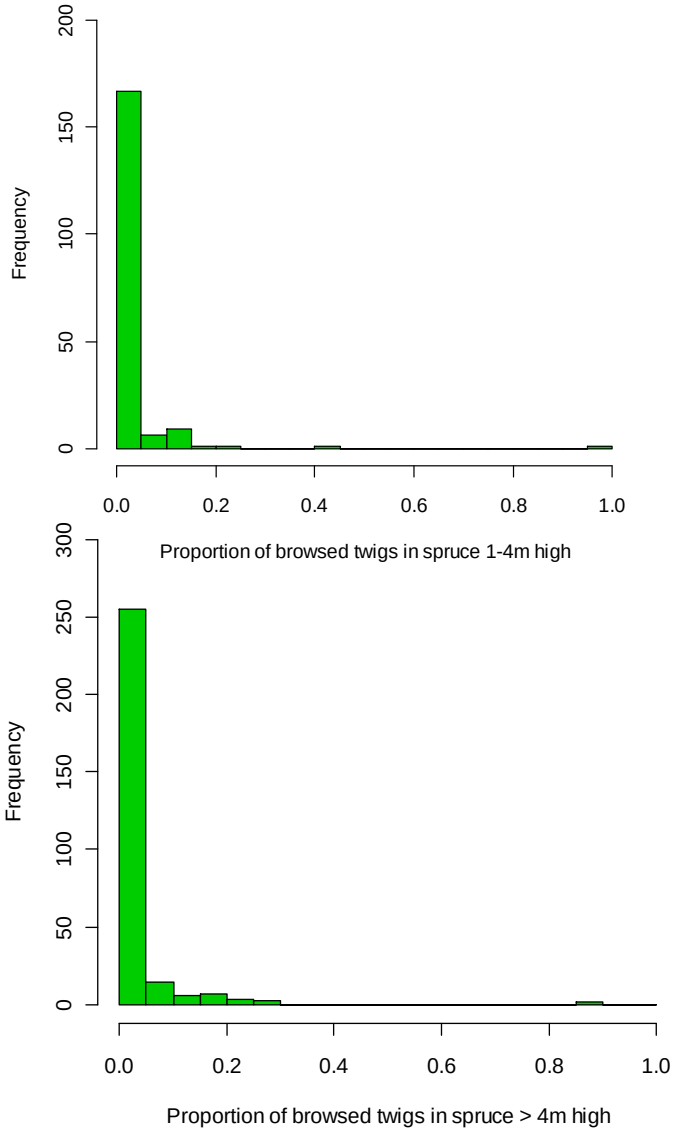


Figure 3a. Histogram representing the frequency of browsed trees. The major part of the trees belonging to this high class did not undergo any browsing. The numbers in the X axis represent the upper interval limits of the browsing proportion of the sampled branches per surveyed tree. Bars were generated in 5% intervals.

In the second height category, i.e. trees 1 – 4 m high, 186 target trees were measured (Fig. 4), and in 371 plots this tree category was not found. A total of 26.3% of the surveyed trees were browsed. The mean browsing proportion per tree was 7.5±7.8% (mean±SD). The mean diameter of the browsed twigs was 2.2±0.6 mm (mean±SD).

Figure 3b. Histogram representing the frequency of browsed trees. The major part of the trees belonging to this high class did not undergo any browsing. The numbers in the X axis represent the upper interval limits of the browsing proportion of the sampled branches per surveyed tree. Bars were generated in 5% intervals.



In the third tree height category (i.e. > 4 m high) a total of 288 trees were measured, and in 269 plots the target tree category was not found. In this category 29.9% of spruces were browsed. The mean browsing per tree was 7.1±5.6% (mean±SD).

Figure 3c. Histogram representing the frequency of browsed trees. The major part of the trees belonging to this high class did not undergo any browsing. The numbers in the X axis represent the upper interval limits of the browsing proportion of the sampled branches per surveyed tree. Bars were generated in 5% intervals.

The mean diameter of the browsed twigs was 1.6±0.4 mm (mean±SD). There were significant differences related with mean diameter between category 1 and 2 ($t = -3.90$, $p < 0.001$; Welch Two Sample t-test), 1 and 3 ($t = 3.87$, $p < 0.001$) and 2 and 3 ($t = 8.15$, $p < 0.001$). In the study area a total of 25.7% of the surveyed trees were affected by browsing.

Modelling browsing on spruce

In regard of the first response variable (trees < 1m), the factors distance to the supplemental feeding site (Pt) and shrub species (BLH) were significantly and near significantly negatively related to the response variable in the 1-factor model, which indicates that the browsing pressure decreased as the distance and the amount of shrubs increased. However, in the maximal model they appeared not significant and were excluded by all model selection procedures (Tab. 2a; 2b).

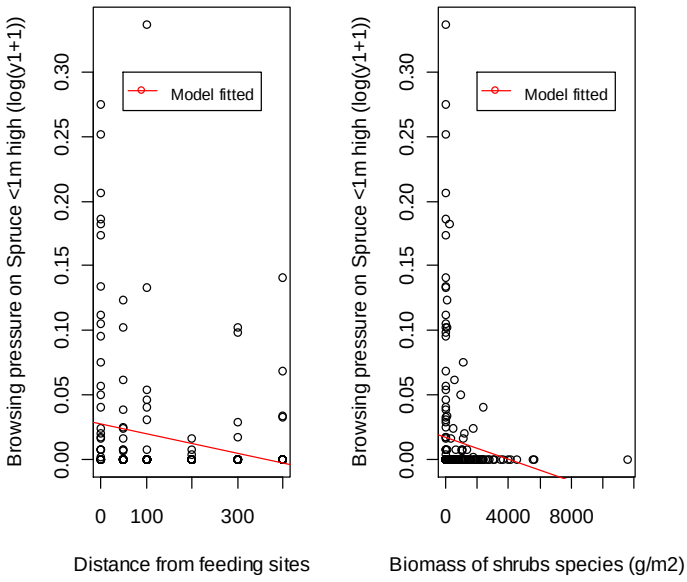


Figure 4. Relation between browsing pressure and both distance from supplemental feeding sites and biomass of shrub species (alternative food). Red line shows 1-factor model fit for the variables compared.

Deciduous tree density (TD) and shape of pine (Sp2) seem to be significant enough for model building and positively related to the response variable, whereas they were not significant in the maximal nor retained by the parsimonious model by any selection method. Likewise, categorical variables such as direction (D), structural complexity (SC) and dominating forest type (FT) were not significant *per se* but they always contained some significant levels (Tab. 2a). Thus, eastern direction was always significant both in 1-factor and maximal models, in contrast to the other cardinal directions. In this light deciduous forest and levels 1 and 2 of structural complexity had a positive and significant and nearly significant relationship with the response, respectively. Consequently, browsing pressure might differ among forest type and structure, although they are not the main factors to explain browsing on spruce (<1m).

Moreover, the parsimonious model selected (Appendix VII), highlights the importance of the shape of spruce (S2) and browsing proportion of pine (Bp2) (Tab. 2b). Both variables have a positive significant effect on the browsing pressure on spruce.

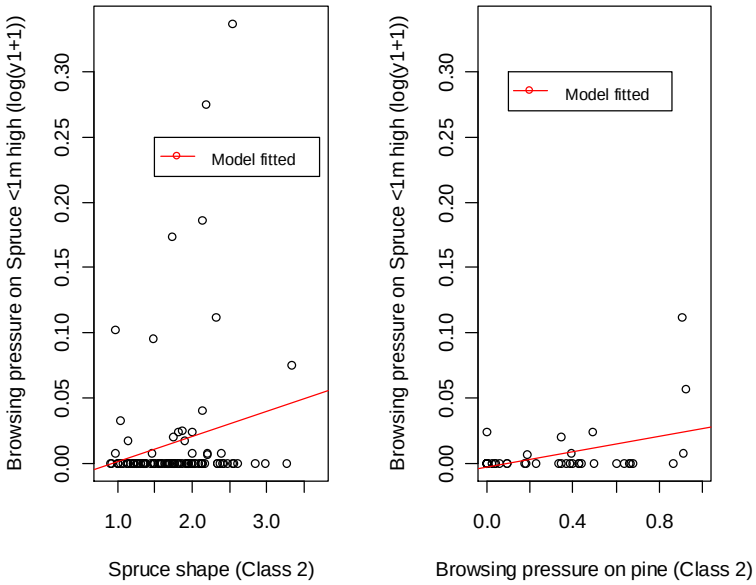


Figure 5. Relation between browsing pressure on spruce (< 1m) and the variables that best explains the occurrence i.e. spruce shape (Class 2) and browsing pressure on pine (Class 2). The red line shows the fit of the 1-factor model for each variable.

Both variables were kept by all model selection procedures (Tab. 2b) explaining more than 40% of the variability of the response variable.

Table 2a. Models at plot scale for the first category of response variables, i.e spruce < 1m high. Log-transformed +1browsing proportion is modelled as a function of the covariates listed in the first column. All factors were tested by 1-factor model. Factors marked in bold were also included in the maximal model. *significant factor, º nearly significant factor. For explanation of the model simplification see Methods

Tested variables		1-factor model			maximal model		
		Estimate	P	P model	estimate	P	P model
Direction	**North**	0.032	0.261	0.203	-0.049	0.509	0.018*
	South	0.040	0.040*		-0.049	0.736	
	East	0.023	0.001*		-0.055	0.027*	
	West	0.028	0.515		-0.049	0.559	
Deer station		0.002	0.694				
Distance to Fd.St (Pt)		-8e-05	0.001*		7e-06	0.881	
Shape of spruce class 1		0.003	0.423				
Shape of spruce class 2		0.019	0.047*		2e-02	0.019*	
Shape of spruce class 3		0.021	0.102				
Browsing on pine class 1		0.005	0.818				
Browsing on pine class 2		0.029	0.003*		5e-02	0.005*	
Browsing on pine class 3		-0.017	0.570				
Shape of pine class 1		3e-04	0.951				
Shape of pine class 2		0.005	0.164		7e-03	0.121	
Shape of pine class 3		0.010	0.240				
Shrubs species (BLH)		-4.e-06	0.079º		-2e-06	0.231	
Deciduous tree density		0.013	0.200		2e-02	0.294	
Structural Complexity	SC 1	0.023	0.001*	0.433			
	SC 2	0.037	0.061º				
	SC 3	0.030	0.359				
	SC 4	0.032	0.480				
	SC 5	0.038	0.344				
Dominating forest type	Spruce forest	0.065	0.222	0.501			
	Pine forest	0.067	0.206				
	Mixed coniferous forest	0.070	0.165				
	Mixed deciduous forest	0.051	0.658				
	Deciduous forest	0.040	0.049*				

Table 2b. The most parsimonious models created by 5 different model selection procedures are presented. The log-transformed y1+1 browsing proportion is modelled as a function of the covariates listed in the second column. The Coefficient of determination and degrees of freedom for each model are also shown in the third and fourth column. P-values of the F-statistic for parsimonious candidate models are also listed on the fifth column. The model marked in bold is selected as the most appropriate to describe the relation with the response variable (see Methods). D: direction; S2: shape of spruce second class; Bp2: browsing proportion of second class pine trees; Sp2: shape of pine second class.

	Parsimonious model	Adj R^2	df	P value	Intercept
Mallows Cp	S2+Bp2+Sp2	0.481	23	< 0.001	yes
Stepwise selection	Bp2	0.239	42	< 0.001	no
Cross-Validation	D+S2+Bp2	0.412	22	< 0.001	yes
Akaike Criterion	S2+Bp2+Sp2	0.481	23	< 0.001	yes
Parsimony	**S2+Bp2**	**0.415**	**25**	**< 0.001**	**yes**

For the second response variable (spruce trees 1-4 m), five factors appeared to be important explaining the browsing pressure on spruce (Tab. 3b), whereas browsing pressure on pine (Class 1) and shape of pine (Class 1) were not considered. Browsing pressure on pine (Class 1) was highly correlated with the covariate browsing pressure on pine (Class 2), and the factor shape of pine (Class 1) had a severe lack of data (Appendix V). Therefore, they were examined by 1-fator model (Tab. 3a & Fig. 6a; 6b).

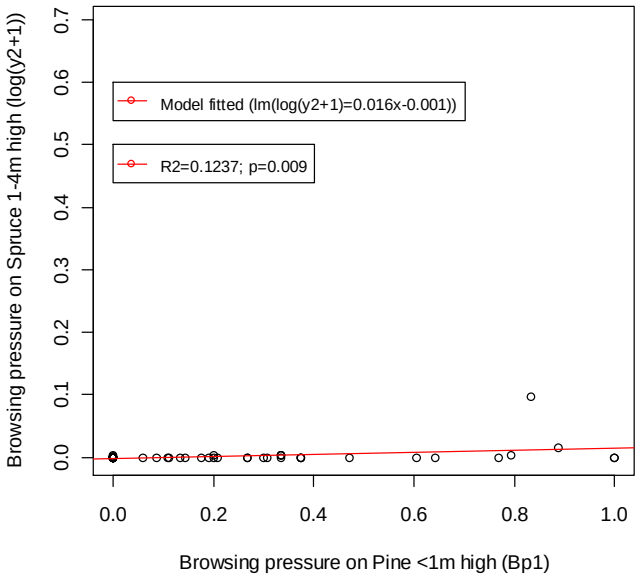


Figure 6a. Relation between browsing pressure on spruce (Class 2) and browsing pressure on pine (Class 1). The legend shows the fitted model, its explanatory power and the model p-value.

Deer station (DS), distance to supplemental feeding site (Pt) and quantity of shrub species (BLH) were related in inverse proportion with the response variable, which indicate that the browsing pressure decreased as they increased. However, only the distance to supplemental feeding site was significant (Tab. 3a). All the mentioned variables were included in the maximal model.

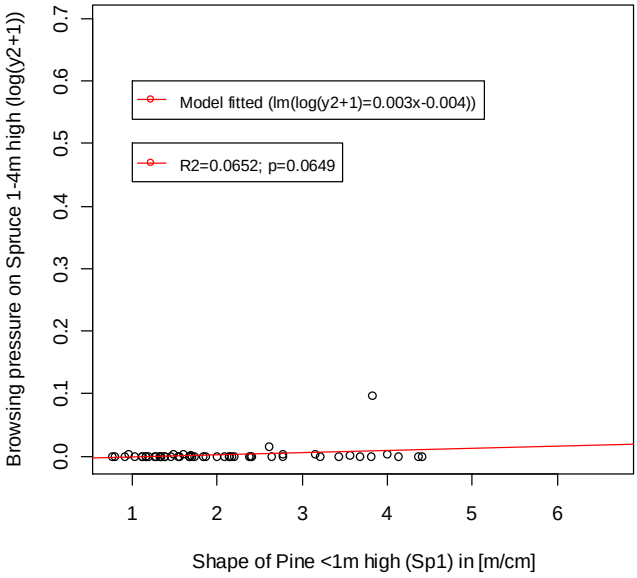


Figure 6b. Relation between browsing pressure on spruce (Class 2) and shape of pine (Class 1). The legend shows the fitted model, its explanatory power and the model p-value.

On the other hand, shape of spruce (Class 2), browsing pressure on pine (Class 2), and structural complexity showed a positive relation with the response variable and were also included in the maximal model, although only browsing pressure on pine (Class 2) was highly significant in both the 1-factor and maximal model (Tab. 3a). Finally, to explain the browsing pressure, two parsimonious models were selected among the potential candidates (Tab. 3b; Appendix VII). In addition, the quantity of shrubs was the only factor dropped by all model selection procedures, indicating the importance of other factors explaining the browsing variability of the response variable. Browsing pressure on pine (Class 2) appeared to be of paramount importance; it showed a positive and highly significant relationship along all the statistical procedures, explaining more than 36% of the response variability.

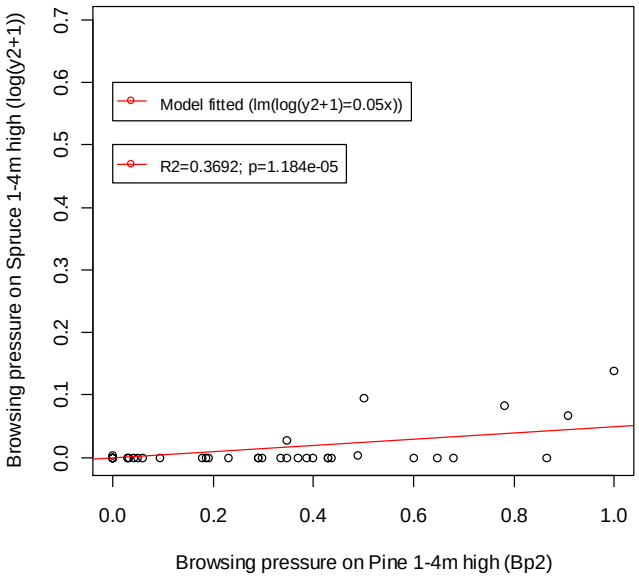


Figure 7. Relation between browsing pressure on spruce (Class 2) explained by browsing pressure on pine (Class 2). The legend shows the fitted model, its explanatory power and the model p-value.

Deer station is a dummy variable negatively related to the response variable, therefore it could be indicative of certain negative interaction regarding areal use of the near vicinity of the feeding sites by fallow deer and wildboar. However, this variable was not significant in the parsimonious model (Tab. 3b; Appendix VII).

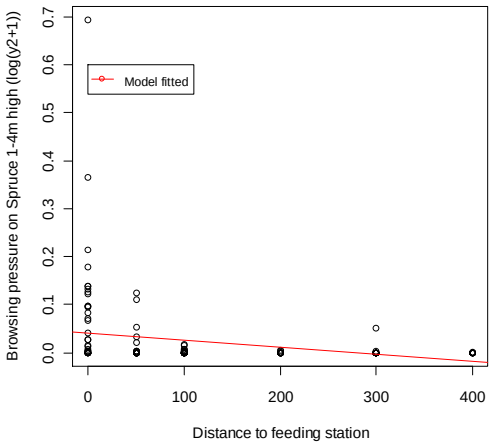


Figure 8. Relation between the response (i.e. browsing pressure on spruce (Class 2)) and the distance to the artificial feeders. Red line represents 1-factor model fitted.

Similarly, distance to feeding sites (Pt) was the only highly significant covariate (negatively related) in the parsimonious model (Appendix VII), whereas shape of spruce (S2) and structural complexity were positively related but not significant (except at the first and forth level of SC).

Table 3a. Models at plot scale of the second category of the response variable, i.e spruce 1-4 m high. Log-transformed +1browsing proportion is modelled as a function of the covariates listed in the first column. All factors were tested by a 1-factor model. Factors marked in bold were also included in the maximal model. *significant factor, º nearly significant factor. For explanation of the model simplification see Methods.

Tested variables		1-factor model			maximal model		
		Estimate	P	P model	estimate	P	P model
Direction	North	0.004	0.681	0.321			0.008*
	South	-0.002	0.385				
	East	0.009	0.312				
	West	-0.017	0.069º				
Deer station		-0.014	0.172		-1e-02	0.175	
Distance to Fd.St (Pt)		-1e-04	0.001*		-2e-05	0.523	
Shape of spruce class 1		0.002	0.404				
Shape of spruce class 2		0.015	0.116		1e-03	0.902	
Shape of spruce class 3		0.018	0.302				
Browsing on pine class 1		0.016	0.009*				
Browsing on pine class 2		0.062	0.001*		5e-02	0.005*	
Browsing on pine class 3		0.033	0.332				
Shape of pine class 1		0.003	0.065º				
Shape of pine class 2		0.003	0.550				
Shape of pine class 3		-0.006	0.662				
Shrubs species (BLH)		-4e-06	0.145		-1e-06	0.469	
Deciduous tree density		-0.013	0.464				
Structural Complexity	**SC 1**	0.027	0.015*	0.127	0.030	0.247	
	SC 2	0.037	0.491		0.055	0.145	
	SC 3	0.047	0.134		0.056	0.132	
	SC 4	-0.004	0.156		0.074	0.027*	
	SC 5	0.038	0.682		0.051	0.470	
Dominating forest type	Spruce forest	0.066	0.542	0.472			
	Pine forest	0.076	0.365				
	Mixed coniferous forest	0.085	0.245				
	Mixed deciduous forest	0.060	0.706				
	Deciduous forest	0.045	0.179				

Table 3b. Parsimonious models created by 5 different model selection procedures are presented. The log-transformed y2+1 browsing proportion is modelled as a function of the covariates listed in the second column. The Coefficient of determination and degrees of freedom for each model are also shown in the third and fourth column. P-values of the F-statistic for parsimonious candidate models are also listed on the fifth column. The model marked in bold is selected as the most appropriate to describe the relation with the response variable (see Methods). DS: deer station; S2: shape of spruce second class; Bp2: browsing proportion of second class pine trees; Pt: distance from the supplemental feeding site; SC: structural complexity of the plot (multi-layered stand).

	Parsimonious model	Adj R^2	df	P value	Intercept
Mallows Cp	Pt+Bp2+SC	0.397	34	< 0.001	no
Cross-Validation	**DS+Pt+S2+SC**	**0.168**	**174**	**< 0.001**	**no**
Stepwise selection	**Bp2**	**0.369**	**40**	**< 0.001**	**no**
Akaike Criterion	Pt+Bp2+SC	0.397	34	< 0.001	no
Parsimony	Bp2	0.369	40	< 0.001	no

Finally, the browsing pressure on spruce trees > 4 m, three variables appeared to play a crucial role; distance to supplemental feeding sites, shape of spruce (Class 3) and structural complexity. Therefore they were kept in the parsimonious model selected (Tab. 4b; Appendix VII). The former was negatively related to the response as well as the latter, in contrast to the shape of spruce whose effect was positive and significant (Fig. 9).

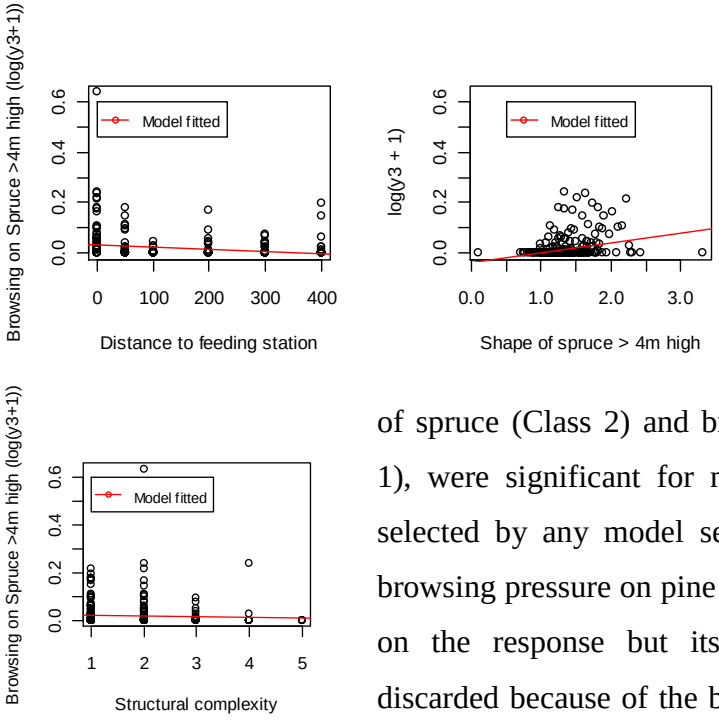


Figure 9. Relation between the factors kept in the parsimonious model and the response variable, in 1-factor models. Red line express its graphical relationship.

Moreover, another three factors such as quantity of shrub species (BLH), shape of spruce (Class 2) and browsing pressure on pine (Class 1), were significant for model building purpose but not selected by any model selection procedures. In contrast, browsing pressure on pine (Class 1) had a significant effect on the response but its inclusion for modelling was discarded because of the bias produced in the model (Tab. 4a).

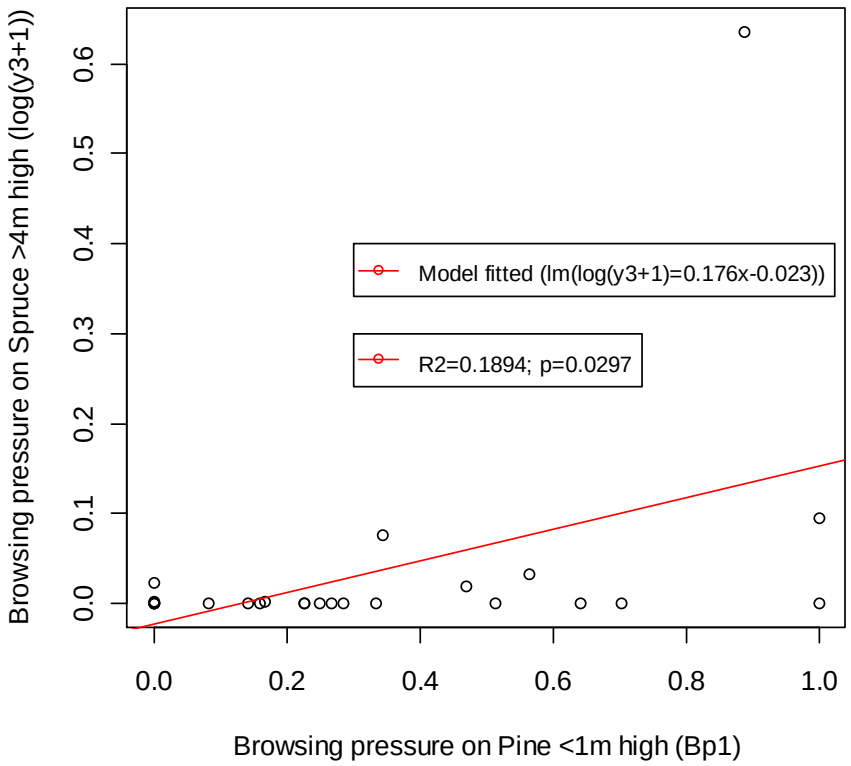


Figure 10. Relation between browsing pressure on spruce (Class 3) explained by browsing pressure on pine (Class 1). The legend shows the fitted model, its explanatory power and the model p-value.

Nevertheless, this variable explained almost 20% of the browsing pressure in spruce (Class 3) and therefore it must be taken into account as an important driver. On the other hand, this response category is the less important in terms of management strategies and economic consequences, because tree growth rates and wood quality of the trees belonging to this category are no longer significantly affected by browsing.

Table 4a. Models at plot scale for third category of response variable, i.e spruce > 4m high. Log-transformed +1browsing proportion is modelled as a function of the covariates listed in the first column. All factors were tested by 1-factor model. Factors marked in bold were also included in the maximal model. *significant factor, º nearly significant factor. For explanation of the model simplification see Methods.

Tested variables		1-factor model			maximal model		
		Estimate	P	P model	estimate	P	P model
Direction	North	0.032	0.518	0.708			0.056
	South	0.036	0.265				
	East	0.026	0.001*				
	West	0.035	0.356				
Deer station		-0.002	0.761				
Distance to Fd.St (Pt)		-9e-05	0.001*		-6e-05	0.022	
Shape of spruce class 1		-0.002	0.832				
Shape of spruce class 2		0.023	0.187		-4e-03	0.556	
Shape of spruce class 3		0.038	0.001*		1e-02	0.284	
Browsing on pine class 1		0.176	0.030*				
Browsing on pine class 2		0.005	0.238				
Browsing on pine class 3		-0.010	0.773				
Shape of pine class 1		0.012	0.617				
Shape of pine class 2		-0.001	0.652				
Shape of pine class 3		0.011	0.236				
Shrubs species (BLH)		-8e-06	0.089º		-2e-06	0.520	
Deciduous tree density		-0.009	0.625				
Structural Complexity	**SC 1**	0.019	0.001*	0.232	0.010	0.618	
	SC 2	0.009	0.185		-0.009	0.056	
	SC 3	0.031	0.199		0.010	0.967	
	SC 4	0.016	0.837		0.001	0.578	
	SC 5	0.038	0.429		0.005	0.798	
Dominating forest type	Spruce forest	0.052	0.590	0.624			
	Pine forest	0.052	0.592				
	Mixed coniferous forest	0.040	0.862				
	Mixed deciduous forest	0.040	0.868				
	Deciduous forest	0.034	0.302				

Table 4b. Parsimonious models created by 5 different model selection procedures are presented. The log-transformed y3+1 browsing proportion is modelled as a function of the covariates listed in the second column. The Coefficient of determination and degrees of freedom for each model are also shown in the third and fourth column. P-values of the F-statistic for parsimonious candidate models are also listed on the fifth column. The model marked in bold is selected as the most appropriate to describe the relation with the response variable (see Methods). Pt: distance from supplemental feeding site; S2: shape of spruce second class; S3: shape of spruce third class; SC: structural complexity of the plot (multi-layered stand).

	Parsimonious model	Adj R^2	df	P value	Intercept
Mallows Cp	**Pt+S3+SC**	**0.235**	**275**	**< 0.001**	**no**
Stepwise selection	Pt	0.051	286	< 0.001	yes
Cross-Validation	Pt+S2+S3	0.161	70	< 0.001	no
Akaike Criterion	Pt+S3+SC	0.235	275	< 0.001	no
Parsimony	Pt+S3+SC	0.235	275	< 0.001	no

Discussion

Browsing pressure around supplemental feeding sites

In the area around the supplemental feeding sites surveyed i.e. in a radius of 400 m from each feeding site selected, a total of 25.7% of the spruce target trees were browsed. By height categories (as the response were classified), 20.5% of spruce < 1 m, 26.3% of spruce 1-4 m and 29.9% of spruce trees > 4 m, underwent browsing with a mean *ca*. 8% per tree. Similar results were reported by Moore et al. (2000) for fallow deer on broadleaved species at the peak of summer consumption. This suggest that the high browsing occurrence on spruce in winter conditions (not preferred species), might be related with the high fallow deer density and supplemental food quality that occurred in the study area. In this line, an increment of spruce browsing across spatiotemporal scales around supplemental feeding sites have been shown for moose (van Beest et al. 2010), proponing that when more preferred species are less abundant, it could cause the inclusion of spruce into the moose diet (Faber & Pehrson 2000). In addition, it has been suggested that the temporal increase of spruce consumption around artificial feeders could be related with a higher demand of roughage to equilibrate the intake of the forage supplied (Doenier et al. 1997).

The results indicated a lower occurrence of browsing in smaller size trees, compared with the other two categories. This is in contrast with our hypothesis in which smaller trees were expected to undergo a higher browsing pressure because they could be reached by all sympatric herbivore species in the area. One plausible explanation could be related to the higher content of secondary metabolites as a protection mechanism of plants against herbivores (Stahl 1888 in Rhoades 1979). For instance, a positive relationship has been shown between higher levels of nitrogen in foliage with a higher susceptibility to browsing (for review see Gill 1992), and even the detection potential of roe deer and moose related with differences in foliage nutrient levels (Gill 1992). However, these defenses are costly due to the resultant diversion of nutrient allocation and energy (Rhoades 1979), with the consequent affection on growth rate. Tree growth can also be halted by browsing, as reported by Bergquist et al. (2003) on Norway spruce (*Picea abies*) where height growth reduction was linearly correlated with the number of years in which the simulated browsing was applied.

The present results indicated a higher browsing pressure in the near vicinity of the supplemental feeding sites, with a declining probability with increasing distance (Fig. 4, 8 and 9), as predicted by central-place foraging theory (Schoener 1979; Rosenberg & McKelvey 1999). The variable distance has been identified as an important factor with a significant effect on the browsing occurrence. It was kept by all model selection procedures for each response category except when applied to smaller size trees. In smaller size trees it was significant in a 1-factor model but not in combination with other factors, nor kept by any model selection procedures in the parsimonious candidates related to the first response category.

The present results are in accordance with other studies (e.g. Guillet et al. 1996; Doenier et al. 1997) showing that supplemental feeding sites represent a focal attraction for cervids and consequently, promoting a restricted spatial use of habitat. The same pattern was pointed out by van Beest et al. (2010) who showed that moose concentrated their movements in a range of 1 km radius around supplemental feeding sites. On the contrary, an increment in browsing pressure as distance increased (up to 900 m) was reported for white-tailed deer around recently established feeding sites, whereas it remained fundamentally constant around the control locations (Doenier et al. 1997). In conclusion, the effect of supplemental feeding sites in relation to browsing is still unclear, and might be associated with the herbivore species and the spatial and temporal scales considered (Gundersen et al. 2004; van Beest et al. 2010).

Factors affecting the browsing occurrence

The results presented here indicate that browsing pressure on pine is the most important factor explaining the variation of browsing on spruce, although its inclusion in the maximal models was not always possible due to auto-correlation or lack of data and subsequent model power reduction. Thus, they have been normally tested individually in 1-factor models. For the first and second (y1 and y2) response variables, browsing pressure on pine (Class 2) has a significant positive influence on both responses. Browsing pressure on pine (Class 1) however, has a positively significant relation to the second and third responses (y2 and y3). The browsing pressure on pine (Class 3) never appears to be relevant for explaining the variability of any response nor kept by any model selection procedure. One may think that the existence of other preferred species

i.e. alternative food, should reduce the pressure subjected on less palatable ones, but surprisingly the results suggested the opposite effect. A possible explanation of this effect could be related to deer density and intra-specific competition as concluded by Schmitz (1990), where competition among white-tailed deer at feeders forced individuals to consume natural browse. These social interactions have been demonstrated for artificially supplemented white-tailed and red deer populations in winter time, and for moose around mineral licks during summer (Ozoga 1972; Veiberg et al. 2004; Courtier & Barrette 1988). Since the most abundant deer species in the study area is the gregarious fallow deer, such interaction ultimately determined by the hierarchical status of the individuals within the herd, would force the less ranked ones to consume natural browse, with the consequent selection of the most preferred or palatable species among the available (Danell et al. 1991; Gill 1992). Another possible explanation is suggested by Palmer et al. (2003). In this study it was demonstrated that preferred plant species attract herbivores and as a consequence the neighboring plant species received a higher impact than expected *a priori*, which also would explain the present results.

Alternative forage, illustrated in the present study by the factor biomass of shrub species (the sum of blueberry, lingonberry and heather) was nearly significant in relation with the three response variables in 1-factor models. It was always included in the maximal model but never retained in any parsimonious, highlighting its relative importance in combination with other factors. Even with a non-significant effect on the response, it showed an inversely relation with it, i.e. an increment of the amount of shrub species implies a reduction in the browsing pressure on the target species. It is not clear however, why it is not an important factor as *a priori* expected. For instance, for red and roe deer browsing on Sitka spruce, a negative relation to the cover of ericoid shrubs was found (Welch et al. 1991). Nevertheless, in an analysis of the rumen content of fallow deer carried out in the study area to determine the deer food choice and preferences, the mentioned three dwarf-shrubs species were an important constituent of the winter diet, representing up to 15% of the total consumption (A. Kastensson, unpubl. data). The lack of significance of this effect could be related with the scarce occurrence of the species due to their high preference by the herbivore fauna, which occur at the study site at an extremely high density, resulting in a less diverse and structural simpler habitat. Another plausible explanation can be associated with having had only one year of data

sampling, as a result, variable winter severity (snow cover), was not considered nor revealed. Moreover deciduous tree density which was also considered here as an alternative food source, did not exert any significant effect related to browsing. This is presumably due to the deer seasonal summer preference and consumption (Miller et al. 1982; Klein et al. 1989; Maizaret & Ballon 1990), with some exceptions such as willow *Salix* sp. that can contribute significantly to red deer and roe deer winter diet (Szmidt 1975; Jamrozy 1980).

Surprisingly, the categorical factor dominating forest type was never significantly related with any of three response variables, in contrast with the findings of Vyšínová (2010) where following a similar multi-variate modelling approach, this factor was one of the most important to explain the winter browsing pressure on pine by moose. On the other hand, structural complexity (multi-layered stand) appeared as an important factor accounting for the variation of the response variables, with the exception of the small spruce trees (< 1m), for which this variable did not show any significant effect. For medium and large spruce trees this factor was part of the most parsimonious models selected, with an apparent effect of browsing reduction as forest stand structure increased. However, this factor should be examined with caution since some levels are composed by only a few observations (levels 4 and 5 occur seldom when describing the forest stands around the plots, so these levels in the independent variable SC contained few values) and could, in consequence, lead to a misinterpretation of the results. According to the present results, Völk (1999) established a correlation between low frequencies of damage and near natural forest (multi-layered) due to the higher abundance of available forage. Stands subjected to heavy browsing normally exhibit a structural bias towards medium and large trees (for review see Gill 1992). This may also restrict the natural regeneration of once common tree species as shown for Canada yew (*Taxus canadensis*), eastern hemlock (*Tsuga canadensis*) and eastern white cedar (*Thuja occidentalis*) in the north-central states in the USA (Alverson, Waller & Solheim (1988) in Andrén & Angelstam (1993)).

In contrast, the opposite effect has also been noted. Fallow deer can have a patchy impact, facilitating the maintenance of small openings in the forest which could contribute to increase the structural diversity (for review see Gill 1992b). In conclusion, the effect of deer browsing seems to be related with its abundance (deer density) and the

vulnerability and density of the plant species (Gill 1992b). Perhaps the best example to illustrate the effect of deer density was provided by Tilghman (1989) who designed an experiment creating five different enclosures for white-tailed deer at various fixed densities (from 0 to 31 deer per km^{-2}) for five years. After the experimental period, he observed a decline in the diversity of browse sensitive species in enclosures with high deer density, and therefore browse resistant species could become dominant. This study also suggests a curvilinear vegetation response to browsing, setting a density threshold (15.5 deer per km^{-2}) from which the effect of deer on vegetation was apparent. In the present study area the deer density, only accounting for fallow deer, is higher than the maximum tested by Tilghman (1989), and consequently a strong impact on vegetation structure and composition may be expected.

The results presented here have also shown the importance of the spruce tree shape, specially medium and large size, to explain the variation of the response variables. Likewise the factor shape of spruce (Class 2) was kept in the parsimonious models of both first and second response high tree classes, whereas spruce shape (Class 3) was associated just with the third (y3) response variable. In any case, this parameter was positively related with the responses, which might suggest a certain kind of attraction or browsing promotion based on the tree`s shape. Danell et al. (1991) conclude that the "foraging decisions [by moose] are made at the tree level", focus more on the morphology of twigs and plants than on measures of nutritional quality (Shipley et al. 1998). At the same time, the shape of the trees can be related to the browsing intensity as well as browsing can be associated to an induced change in the nutritional quality of the twigs, by diverting compound allocation or generation of induced second metabolites. Thus, in the case of conifers, it can be expected that non-browsed trees could exert a greater attraction for herbivores by deer association of a certain shape with higher nutritional quality, and consequently trigger the feed selection by deer. To support this hypothesis it has been reported also for moose and other browsers about the capability of discrimination of pine browse based on its nitrogen content (Ball et al. 2000) that secondary metabolites can influence diet choice and that its production by plants is a functional response to damage or browsing intensity (for review see Gill 1992). In this regard, it has also been suggested that trees with a previous browsing history are more susceptible to new browsing, whereas at branch scale, previously

browsed twigs are usually avoided as a consequence of the above mentioned induced plant defences (for review see Coté et al. 2004).

In addition, the potential areal interference or interaction between fallow deer and wild boar was also aimed to be tested. This factor was only kept in the most parsimonious model concerning the second response variable, i.e. trees 1-4 m high, in which a negative relation with the response was shown, although this factor appeared non-significant in the model, and as a consequence, interpretation should be done with caution. Nevertheless the sign of the estimate could be expressing a certain kind of areal interference and the subsequent reduction of browsing on the target trees.

In conclusion there were four main factors explaining the variation of browsing pressure on spruce trees. These factors were: distance from the supplemental feeding sites, browsing pressure on pine, spruce shape and structural complexity. The high browsing values found on spruce were caused by both the attraction exerted by the supplemental feeding sites and by the high deer density present in the area, even though supplemental food was provided *ad libitum*. However, these results could be affected by the existence of other deer species in the area, for which its interpretation must be done with caution.

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Appendix I. Habitat composition at Koberg study area.

Habitat type	*Habitat composition in study area (%)*
Solitary houses with property	0.33
Non-urban parks	0.36
Arable land	12.46
Pastures	3.97
Broad-leaved forest not on mires	3.37
Broad-leaved forest on mires	0.10
Coniferous forest on lichen-dominated areas	2.51
Coniferous forest 5-15 m	15.24
Coniferous forest >15 m	28.79
Coniferous forest on mires	5.86
Coniferous forest on open bedrock	0.46
Mixed forest not on mires	5.69
Mixed forest on mires	0.02
Clear-felled areas	9.97
Younger forest	6.87
Mires and marshes	1.72
Lakes and ponds open surface	1.15
Lakes and ponds surface being grown over	0.85

Appendix II. Branch Classification

This classification was crucial in order to calculate the proportion of browsed twigs upon spruce trees. The table shows the five branches of each class sampled to estimate the mean number of twigs contained in each class. The Standard Deviation of the measurements is also provided.

Class 0	***Class 1***	***Class 2***	***Class 3***	***Class 4***	
0	110	215	548	821	
0	104	340	578	890	
0	147	254	478	966	
0	96	390	523	798	
0	178	267	448	907	
0	**127**	**293,2**	**515**	**876,4**	**mean**
0	**34.6**	**70.5**	**52.4**	**67.8**	**SD**

Table C. Branch Classifcation, number of twigs per branch class.

Class 0. Trees without branches, with dead branches, dried or not available.

Note: The branches were selected from 0.5 to 2 m height.

Appendix III. Conifers Protocol

Observer ----------

……

St. Number and plot----------

Date----------

Coordenates (GPS)……

HABITAT

Forest ☐ **Islet** ☐

Impediment ☐

Clearcut ☐
Plantation; -1m ☐
Young; 1,1-2m ☐
Young; 2,1-5m ☐
Thinning; 5,1-15m ☐
Old growth >15m ☐

Trees (%):

Spruce ☐
Pine
Birch
Aspen
Rowan
Oak
Willow

First Growth Status ☐

Fallow field ☐

Former Pasture ☐

Agric

Clover ☐
Cultivated
Oats
Wheat
Grain
Unspecified
Ploughed ☐

Other: _____

Observations----------

NORWAY SPRUCE (*Picea abies*)

	DCCT	Lead shoot b		Stem br		Bark str		Bark gn	
		Fresh	Old	F	O	F	O	F	O
0-0,99 m									
Height 1-4 m									
> 4 m									

Height 0-0,99 m	% br	TNº tw	Nº tw b	Ø twig	Ø and H

Height 1-4 m	% br	TNº tw	Nº tw b	Ø twig	Ø and H

> 4 m	% br	TNº tw	Nº tw b	Ø twig	Ø and H

SCOTS PINE (*Pinus sylvestris*)

DCCT	Lead shoot b		Stem br		Bark str		Bark gn	
	Fresh	Old	F	O	F	O	F	O

% br	TNº tw	Nº tw b	Ø twig	Ø and H

% br	TNº tw	Nº tw b	Ø twig	Ø and H

% br	TNº tw	Nº tw b	Ø twig	Ø and H

DCCT. Distance from the center of the plot to the closest target tree
Lead shoot b. Leading shoot browsed
Stem br. Stem broken
Bark str. Bark striped tree
Bark gn. Bark gnawed stem
% br. Percentage of twigs browsed
TNº tw. Total number of available twigs
Nº tw b. Number of browsed twigs
Ø twig. Twig diameter
Ø and H. Tree diameter and height

Class 0.
Class 1.
Class 2.
Class 3.
Class 4.

OBSERVATONS……

……

……

Appendix IV. Deciduous trees protocol

Observer ----------

St. Number and plot----------

Start point ……

Date----------

Coordenates (GPS) ……

End point ……

Distance to centroid……

……

Number of target trees along the transect			
1	B.pend	Betula	
2	B.pubs		
3	Salix spp		
4	Oak		
5	Aspen		
6	Others		
Including Tilia cordata, Fraxinus excelsior, Ulmus glabra, Acer platanoides, Sorbus aucuparia			

Sp	H	St br	Dist to 0	Br	Not Br	F	O	Sp	H	St br	Dist to 0	Br	Not Br	F	O

Observations ……

……

H: Trees up to 4 m, and measuring browsing pressure up to 2 m

Appendix V. Correlation Matrix and Outliers detection

Correlation Matrices. Spearman rho Method

An important question is to determine possible collinearity problems between covariates, which can led to type II errors. Consequently I tested for possible correlation levels between the factors potentially included in the model, to avoid the inclusion of strongly correlated variables (correlation coefficient > 0.5) in the same model (Edge et al. 1987).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1:D	1.00										
2:Pt	-0.01	1.00									
3:S2	-0.02	-0.19	1.00								
4:S3	0.09	-0.24	0.08	1.00							
5:Bp2	-0.05	-0.35	-0.05	-0.23	1.00						
6:Sp2	-0.18	-0.10	0.35	0.09	0.04	1.00					
7:Sp3	-0.03	-0.04	0.04	0.38	-0.16	-0.38	1.00				
8:BLH	-0.08	0.03	0.13	-0.08	-0.12	0.04	-0.09	1.00			
9:TD	-0.07	0.02	0.07	-0.04	0.24	-0.09	0.03	0.16	1.00		
10:SC	0.02	0.06	0.09	0.10	-0.07	-0.06	0.18	0.23	0.24	1.00	
11:FT	0.03	-0.02	0.12	-0.07	0.09	0.01	0.03	-0.21	-0.11	-0.13	1.00

Tabla 1a. Spearman Correlation Matrix for the independent variables potentially included in the maximal model of response variable y1.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1:DS	1.00										
2:D	-0.01	1.00									
3:Pt	-0.00	-0.01	1.00								
4:S2	0.13	-0.02	-0.19	1.00							
5:Bp1	0.06	-0.05	-0.20	-0.24	1.00						
6:Bp2	0.05	-0.05	-0.35	-0.05	0.57	1.00					
7:Sp1	-0.03	-0.06	-0.35	0.19	0.16	-0.10	1.00				
8:BLH	-0.10	-0.08	0.03	0.13	-0.29	-0.12	-0.09	1.00			
9:TD	-0.30	-0.06	0.02	0.07	-0.07	0.24	-0.22	0.16	1.00		
10:SC	-0.17	0.02	0.06	0.09	-0.19	-0.07	-0.09	0.23	0.24	1.00	
11:FT	0.14	0.03	-0.02	0.12	-0.04	0.10	0.16	-0.21	-0.11	-0.13	1.00

Tabla 1b. Spearman Correlation Matrix for the independent variables potentially included in the maximal model of response variable y2.

	1	2	3	4	5	6	7	8	9
1:D	1.00								
2:Pt	-0.01	1.00							
3:S2	-0.02	-0.19	1.00						
4:S3	0.09	-0.24	0.08	1.00					
5:Bp1	-0.05	-0.20	-0.24	0.09	1.00				
6:Bp2	-0.05	-0.35	-0.05	-0.23	0.57	1.00			
7:Sp3	-0.03	-0.04	0.04	0.38	-0.14	-0.16	1.00		
8:BLH	-0.08	0.03	0.13	-0.08	-0.29	-0.12	-0.09	1.00	
9:FT	0.03	-0.02	0.12	-0.07	-0.04	0.10	0.03	-0.21	1.00

Tabla 1c. Spearman Correlation Matrix for the independent variables potentially included in the maximal model of response variable y3.

Outlier Detection

According to literature, Cleveland dotplot (Cleveland 1993) is a good graphical method to visualize outliers in a dataset, rather than boxplot. In the present study both methods have been applied.

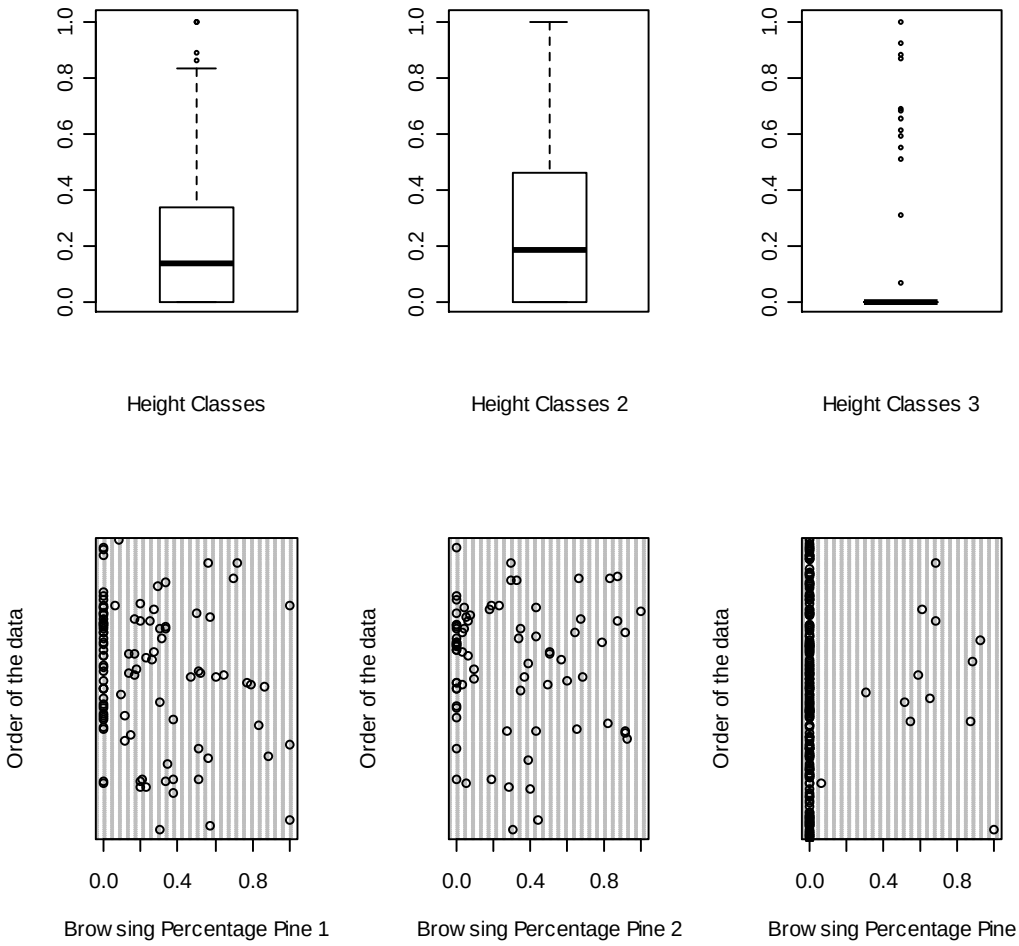


Figure A. Two methods for outlier detection were applied i.e. box-plot and Cleveland dotplot. The upper part shows box-plot applied to each height category of browsing proportion on pine, whereas the lower, Cleveland dotplots were constructed.

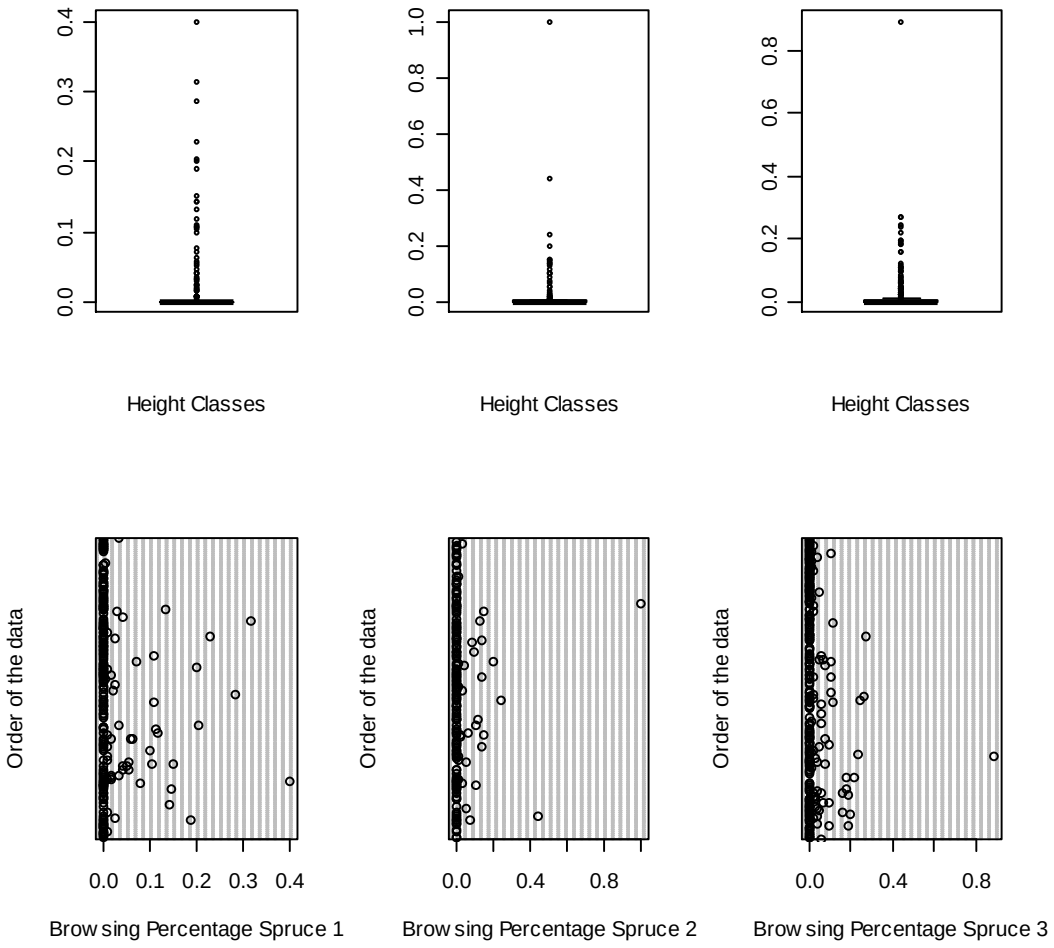


Figure B. Two methods for outlier detection were applied i.e. box-plot and Cleveland dotplot. The upper part shows box-plot applied to each height category of the response variables, browsing proportion on spruce, whereas the lower, Cleveland dotplots were constructed.

Appendix VI. GLM

Generalized Linear Model Approach (GLM)

The approach was to work with GLM's, in which it is necessary to specify the distribution of the data, the link function which describes the relationship between the mean value and the variance in the distribution (see Olsson 2002), and the linear predictor. The choice of distribution affects the assumptions we make regarding variances, since the relation between the variance and the mean is known for many distributions (Olsson 2002). In this case, since the response variable was a proportion (i.e proportion browsed) a Binomial distribution with a logit link was first tested. Due to the nature of the data set with many zero observations, the model using binomial errors did not fit adequately, leading to overdispersion. Thus, a quasi-binomial distribution was used in order to avoid the mentioned statistical problems, specifying a more appropriate variance function, where the dispersion parameter is not fixed (response variable y2 as an example).

```
glm0=glm(y2~DS+D+Pt+S2+Bp2+Sp1+BLH+TD+SC+FT,family=quasibinomial(link="logit"),data=mydata2,na.action=na.omit)
summary(glm0)
```

Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-3.697e+01	1.008e+01	-3.667	0.02144 *
DS	-4.312e+00	2.971e+00	-1.452	0.22023
DN	-5.777e-02	3.632e+00	-0.016	0.98807
DS	-1.059e+00	2.919e+00	-0.363	0.73517
DW	1.102e+01	3.619e+00	3.045	0.03820 *
Pt	4.452e-02	7.841e-03	5.677	0.00475 **
S2	-3.109e+00	3.358e+00	-0.926	0.40698
Bp2	1.599e+00	6.473e+00	0.247	0.81704
Sp1	1.132e+00	1.938e+00	0.584	0.59072
BLH	-1.033e-04	4.661e-04	-0.222	0.83551
TD	6.174e+00	4.538e+00	1.361	0.24528
SC3	-1.806e+00	2.445e+00	-0.739	0.50112
SC4	-1.096e+01	4.170e+00	-2.629	0.05828 .
FTMixed_deciduous_forest	3.028e+01	4.189e+00	7.229	0.00194 **
FTPine_forest	1.057e+01	2.926e+00	3.614	0.02248 *
FTSpruce_forest	5.371e+00	1.840e+00	2.919	0.04328 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 1.039137e-10)
Null deviance: 3.6289e-02 on 19 degrees of freedom
Residual deviance: 3.0592e-10 on 4 degrees of freedom
(537 observations deleted due to missingness)
AIC: NA
Number of Fisher Scoring iterations: 24

One disadvantage of the method is that it is not computing AIC (Akaike Information Criterion; Akaike 1974) values, because the log-likelihood parameter cannot be calculate, so the subsequent model selection procedure was limited. Another limitation is the impossibility to obtain the coefficient of determination, which expresses the amount of variation in the response variable that is explained by the model. The dataset was in this perspective too small and a major limitation for a successful analysis applying the above mentioned method i.e. too many cases with missing values.
In consequence, I opted for finding the best transformation of the response variable to allow for a normal linear regression model to fit the data.

Appendix VII. Model selection procedures and best candidates models

Model Selection Procedures

Parsimony method: Applying parsimony principles I obtained the best candidate model for each response variable.

Response y1. Browsing proportion on spruce trees less than one meter high.

lm(formula = log (y1+1) ~ S2 + Bp2, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.024251	-0.009203	-0.003097	0.006605	0.056115

Coefficients:

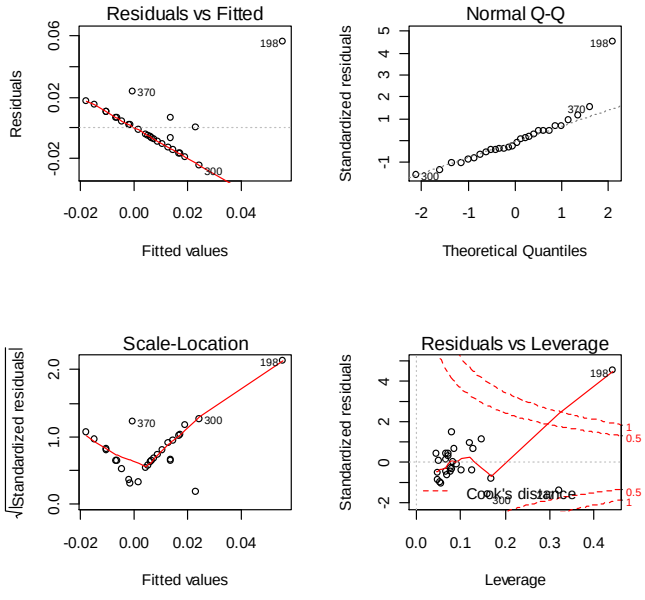
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	-0.039910	0.013153	-3.034	0.005560 **
S2	0.019692	0.006942	2.837	0.008907 **
Bp2	0.054955	0.013384	4.106	0.000377 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.01664 on 25 degrees of freedom
(529 observations deleted due to missingness)
Multiple R-squared: 0.4584, **Adjusted R-squared: 0.415**

F-statistic: 10.58 on 2 and 25 DF, **p-value: 0.0004692**

Diagnostic graphs of the candidate



Response y2. Browsing proportion on spruce trees from one to four meters high.

lm(formula = log (y2+1) ~ Bp2 -1, data = mydata, na.action = na.omit)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.041820	-0.017817	-0.004524	0.000000	0.091166

Coefficients:

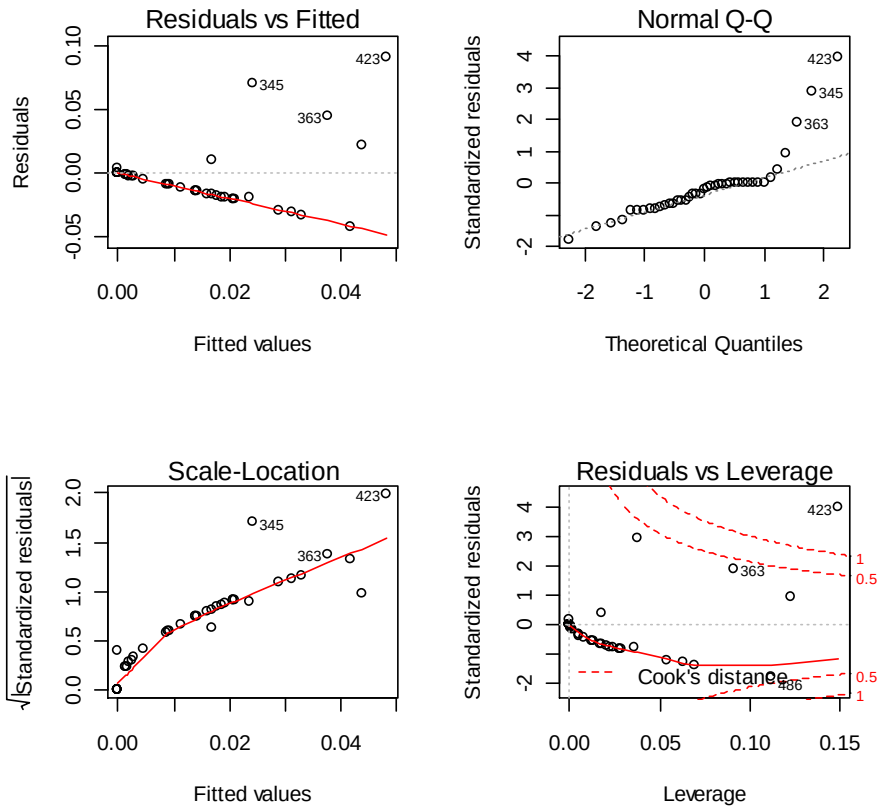
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Bp2	0.048254	0.009651	5	1.18e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.02498 on 40 degrees of freedom
(516 observations deleted due to missingness)
Multiple R-squared: 0.3846, **Adjusted R-squared: 0.3692**

F-statistic: 25 on 1 and 40 DF**, p-value: 1.184e-05**

Diagnostic graphs of the candidate



Response y3. Browsing proportion on spruce trees more than four meters high.

lm(formula = log (y3+1) ~ Pt + S3 + SC - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.071592	-0.020908	-0.009434	0.004589	0.206594

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Pt	-5.888e-05	1.741e-05	-3.383	0.000821 ***
S3	3.426e-02	7.668e-03	4.468	1.16e-05 ***
SC1	-1.726e-02	1.158e-02	-1.490	0.137333
SC2	-1.527e-02	1.249e-02	-1.222	0.222675
SC3	-2.996e-02	1.344e-02	-2.230	0.026571 *
SC4	-1.195e-02	1.682e-02	-0.710	0.477997
SC5	-3.560e-02	1.990e-02	-1.789	0.074693 .

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

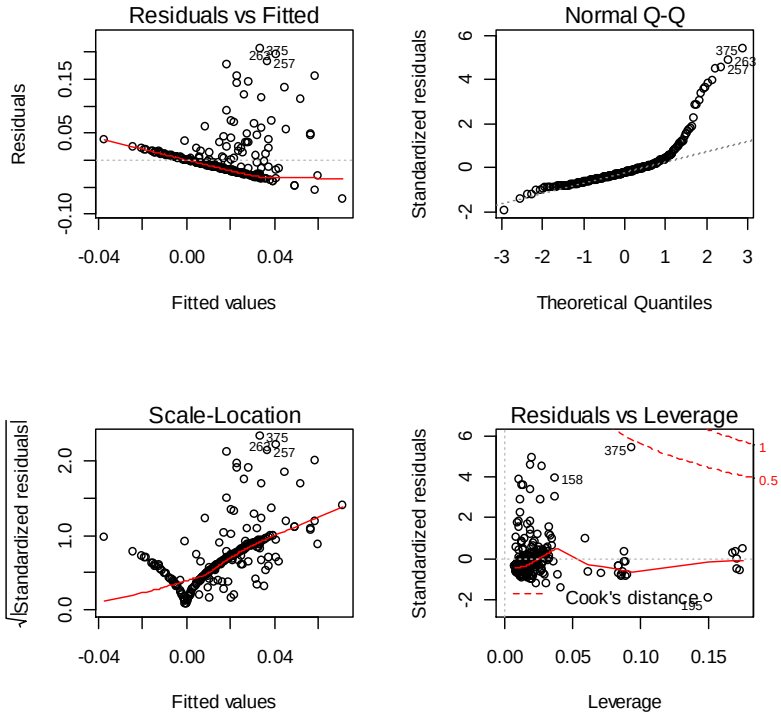
Residual standard error: 0.04033 on 275 degrees of freedom

(275 observations deleted due to missingness)

Multiple R-squared: 0.2536, **Adjusted R-squared: 0.2346**

F-statistic: 13.35 on 7 and 275 DF, **p-value: 8.007e-15**

Diagnostic graphs of the candidate



Mallows Cp method: This procedure produces the first 20 best models.

Here is shown the best of them based in its Cp value.

Response y1

lm(formula = log (y1+1) ~ S2 + Bp2 + Sp2, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.020558	-0.010647	-0.004251	0.007634	0.048737

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	-0.053558	0.014316	-3.741	0.001067 **
S2	0.020073	0.006814	2.946	0.007250 **
Bp2	0.053264	0.012881	4.135	0.000402 ***
Sp2	0.006503	0.003292	1.975	0.060351 .

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

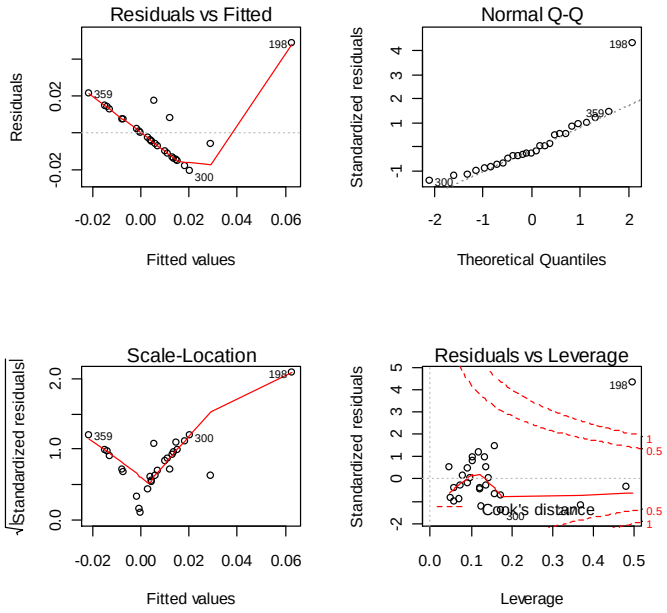
Residual standard error: 0.01598 on 23 degrees of freedom

(530 observations deleted due to missingness)

Multiple R-squared: 0.5405, **Adjusted R-squared: 0.4805**

F-statistic: 9.017 on 3 and 23 DF, **p-value: 0.0003924**

Diagnostic graphs of the candidate



Response y2

lm(formula = log (y2 +1) ~ Pt + Bp2 + SC - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.036879	-0.014950	0.001561	0.009215	0.068559

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Pt	-2.723e-05	3.585e-05	-0.760	0.452726
Bp2	5.880e-02	1.599e-02	3.677	0.000808 ***
SC1	1.472e-02	1.720e-02	0.856	0.398011
SC2	-2.650e-03	9.398e-03	-0.282	0.779688
SC3	-2.779e-03	9.602e-03	-0.289	0.774020
SC4	-2.423e-02	1.614e-02	-1.501	0.142475
SC5	6.332e-03	2.677e-02	0.236	0.814467

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

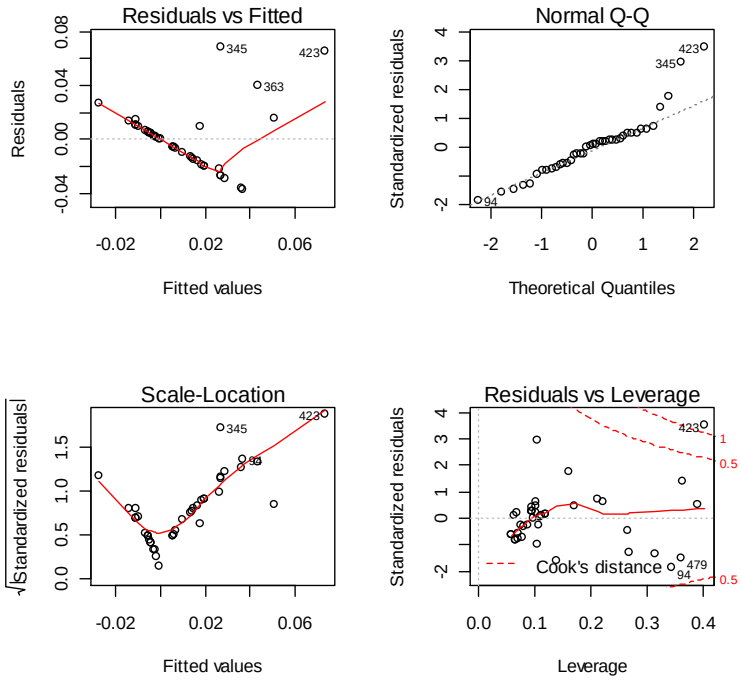
Residual standard error: 0.02443 on 34 degrees of freedom

(516 observations deleted due to missingness)

Multiple R-squared: 0.4998, **Adjusted R-squared: 0.3968**

F-statistic: 4.852 on 7 and 34 DF, **p-value: 0.0007145**

Diagnostic graphs of the candidate



Response y3

lm(formula = log (y3 + 1) ~ Pt + S3 + SC - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.071592	-0.020908	-0.009434	0.004589	0.206594

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Pt	-5.888e-05	1.741e-05	-3.383	0.000821 ***
S3	3.426e-02	7.668e-03	4.468	1.16e-05 ***
SC1	-1.726e-02	1.158e-02	-1.490	0.137333
SC2	-1.527e-02	1.249e-02	-1.222	0.222675
SC3	-2.996e-02	1.344e-02	-2.230	0.026571 *
SC4	-1.195e-02	1.682e-02	-0.710	0.477997
SC5	-3.560e-02	1.990e-02	-1.789	0.074693 .

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

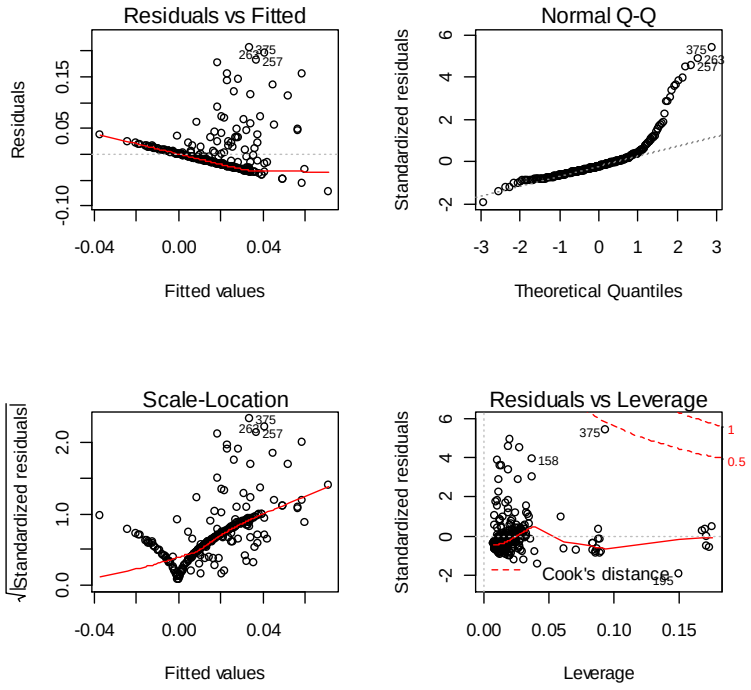
Residual standard error: 0.04033 on 275 degrees of freedom

(275 observations deleted due to missingness)

Multiple R-squared: 0.2536, **Adjusted R-squared: 0.2346**

F-statistic: 13.35 on 7 and 275 DF, **p-value: 8.007e-15**

Diagnostic graphs of the candidate



Stepwise selection method

Response y1

lm(formula = log (y1 + 1) ~ Bp2 - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.021065	-0.010070	-0.001651	0.000000	0.089595

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Bp2	0.024306	0.006377	3.812	0.000445 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

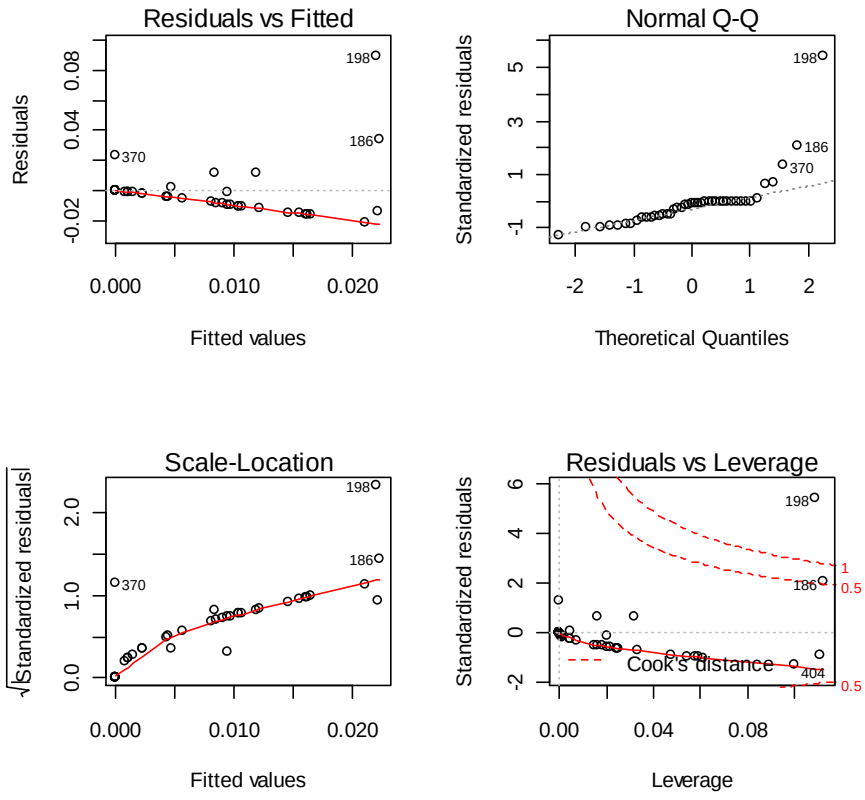
Residual standard error: 0.01751 on 42 degrees of freedom

(514 observations deleted due to missingness)

Multiple R-squared: 0.257, **Adjusted R-squared: 0.2393**

F-statistic: 14.53 on 1 and 42 DF, **p-value: 0.0004448**

Diagnostic graphs of the candidate



Response y2

lm(formula = log (y2 + 1) ~ Bp2 - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.041820	-0.017817	-0.004524	0.000000	0.091166

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Bp2	0.048254	0.009651	5	1.18e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

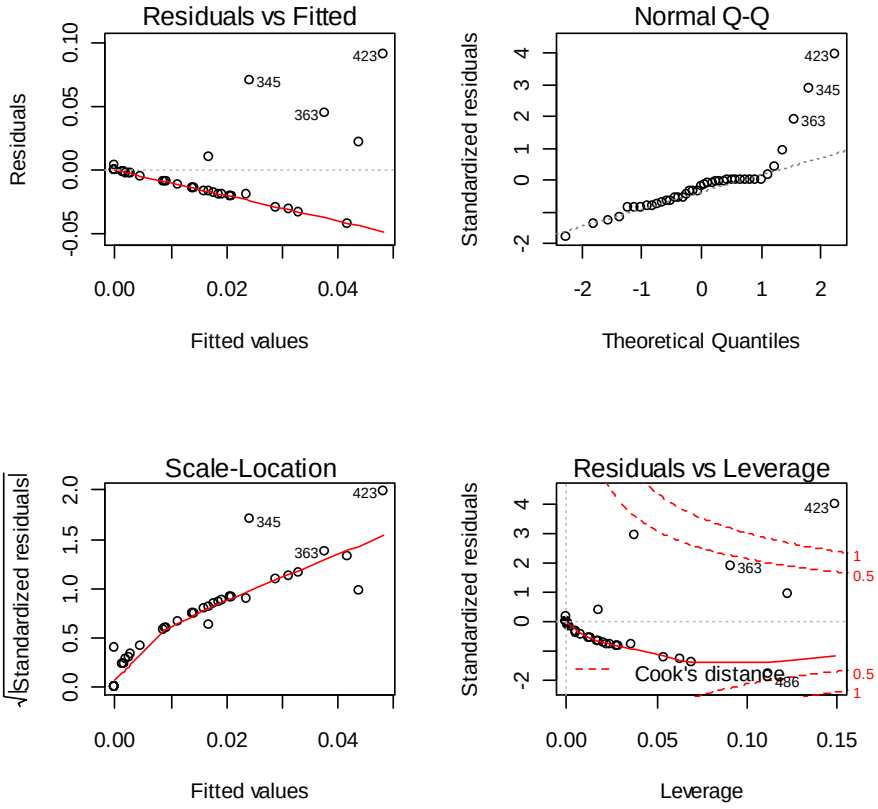
Residual standard error: 0.02498 on 40 degrees of freedom

(516 observations deleted due to missingness)

Multiple R-squared: 0.3846, **Adjusted R-squared: 0.3692**

F-statistic: 25 on 1 and 40 DF, **p-value: 1.184e-05**

Diagnostic graphs of the candidate



Response y3

lm(formula = log (y3 + 1) ~ Pt, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.03558	-0.02641	-0.01025	0.00111	0.60041

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	3.558e-02	5.183e-03	6.865	4.13e-11 ***
Pt	-9.172e-05	2.253e-05	-4.070	6.08e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

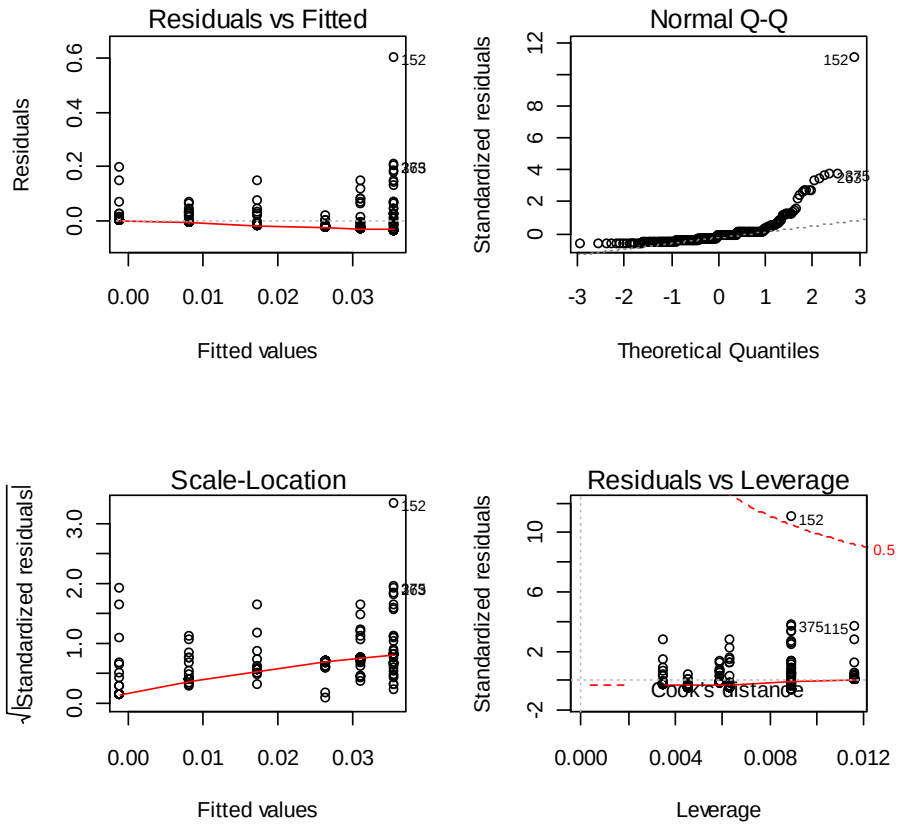
Residual standard error: 0.05475 on 286 degrees of freedom

(269 observations deleted due to missingness)

Multiple R-squared: 0.05476, **Adjusted R-squared: 0.05146**

F-statistic: 16.57 on 1 and 286 DF, **p-value: 6.077e-05**

Diagnostic graphs of the candidate



Cross Validation method : This procedure produces the first 20 best models.

Here is shown the best of them.

Response y1

lm(formula = log (y1+1) ~ D + S2 + Bp2, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.021430	-0.009536	-0.004516	0.009556	0.048887

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	-0.030602	0.015281	-2.003	0.057694 .
DN	-0.010921	0.007959	-1.372	0.183845
DS	-0.010440	0.012099	-0.863	0.397544
DW	-0.012475	0.008468	-1.473	0.154881
S2	0.018756	0.007632	2.457	0.022343 *
Bp2	0.055051	0.013653	4.032	0.000558 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

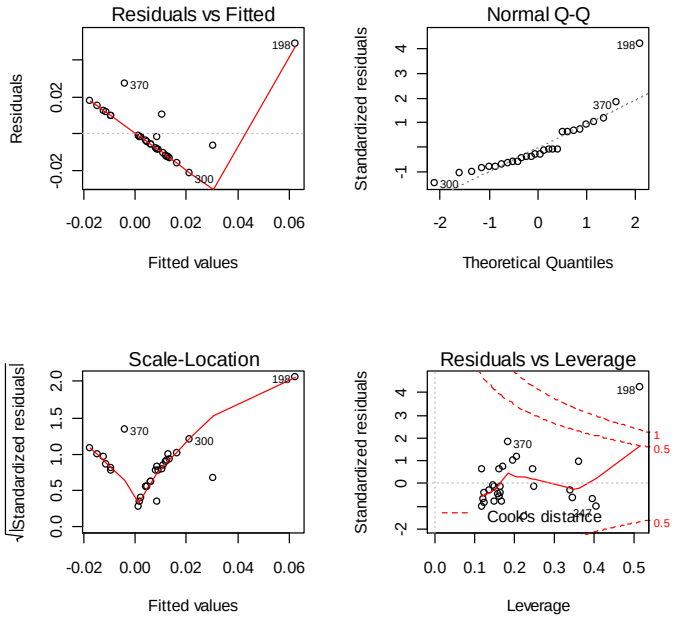
Residual standard error: 0.01668 on 22 degrees of freedom

(529 observations deleted due to missingness)

Multiple R-squared: 0.5212, **Adjusted R-squared: 0.4124**

F-statistic: 4.79 on 5 and 22 DF, **p-value: 0.004111**

Diagnostic graphs of the candidate



Response y2

lm(formula = log (y2+1) ~ DS + Pt + S2 + SC - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.08990	-0.02661	-0.01154	0.01050	0.59579

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
DS (Deer Station)	-1.555e-02	1.002e-02	-1.552	0.122538
Pt	-1.482e-04	3.728e-05	-3.976	0.000103 ***
S2	1.052e-02	9.556e-03	1.101	0.272518
SC 1	4.209e-02	2.037e-02	2.067	0.040256 *
SC 2	2.056e-02	1.984e-02	1.036	0.301618
SC 3	2.002e-02	2.050e-02	0.976	0.330280
SC 4	7.390e-02	2.760e-02	2.678	0.008118 **
SC 5	3.395e-02	2.982e-02	1.138	0.256497

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

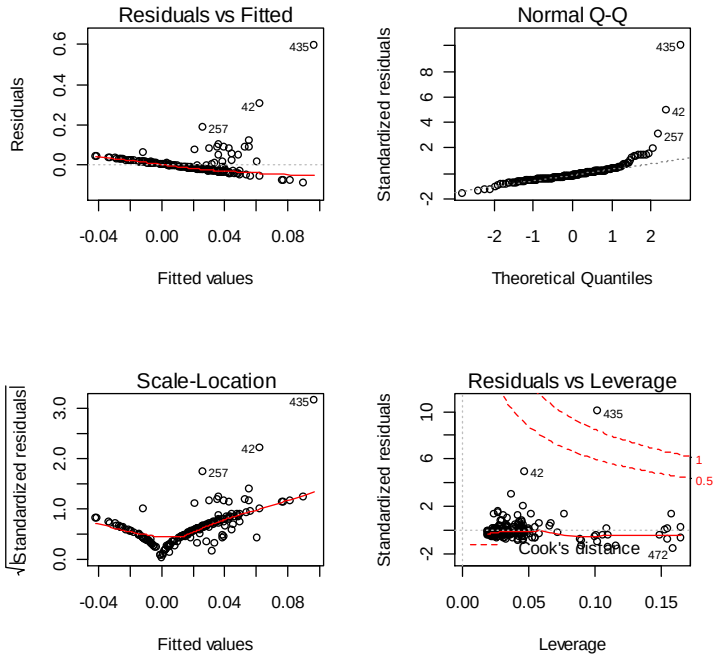
Residual standard error: 0.06277 on 174 degrees of freedom

(375 observations deleted due to missingness)

Multiple R-squared: 0.2043, **Adjusted R-squared: 0.1678**

F-statistic: 5.586 on 8 and 174 DF, **p-value: 2.647e-06**

Diagnostic graphs of the candidate



Response y3

lm(formula = log (y3+1) ~ Pt + S2 + S3 - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.039405	-0.013513	-0.005779	0.005772	0.195991

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Pt	-6.131e-05	2.334e-05	-2.626	0.0106 *
S2	-9.839e-04	5.780e-03	-0.170	0.8653
S3	1.603e-02	6.857e-03	2.338	0.0222 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

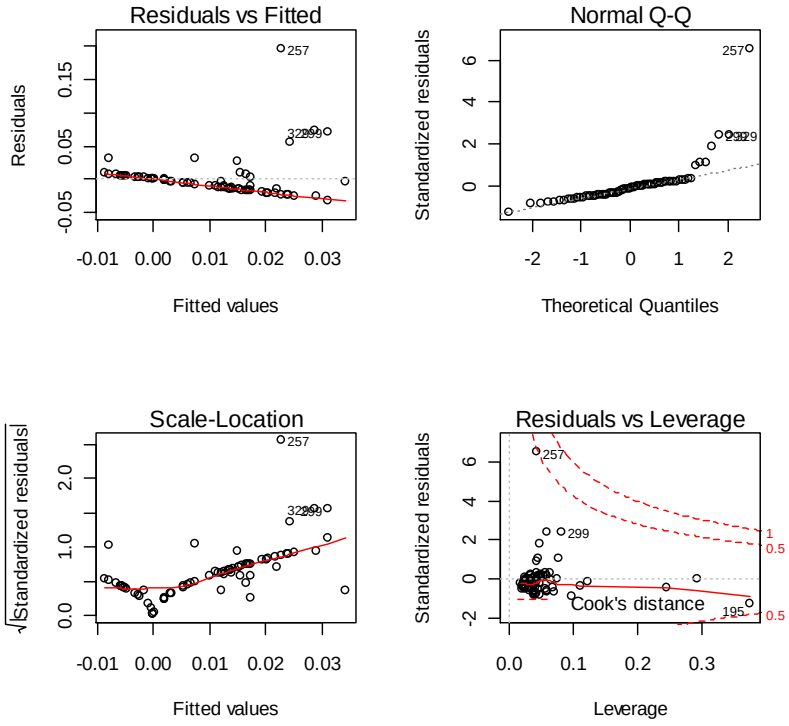
Residual standard error: 0.03056 on 70 degrees of freedom

(484 observations deleted due to missingness)

Multiple R-squared: 0.196, **Adjusted R-squared: 0.1616**

F-statistic: 5.689 on 3 and 70 DF, **p-value: 0.00152**

Diagnostic graphs of the candidate



Akaike Information Criterion

This procedure produces the first 20 best models.

Here is shown the best of them based in its AIC value.

Response y1

lm(formula = log (y1+1) ~ S2 + Bp2 + Sp2, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.020558	-0.010647	-0.004251	0.007634	0.048737

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	-0.053558	0.014316	-3.741	0.001067 **
S2	0.020073	0.006814	2.946	0.007250 **
Bp2	0.053264	0.012881	4.135	0.000402 ***
Sp2	0.006503	0.003292	1.975	0.060351 .

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

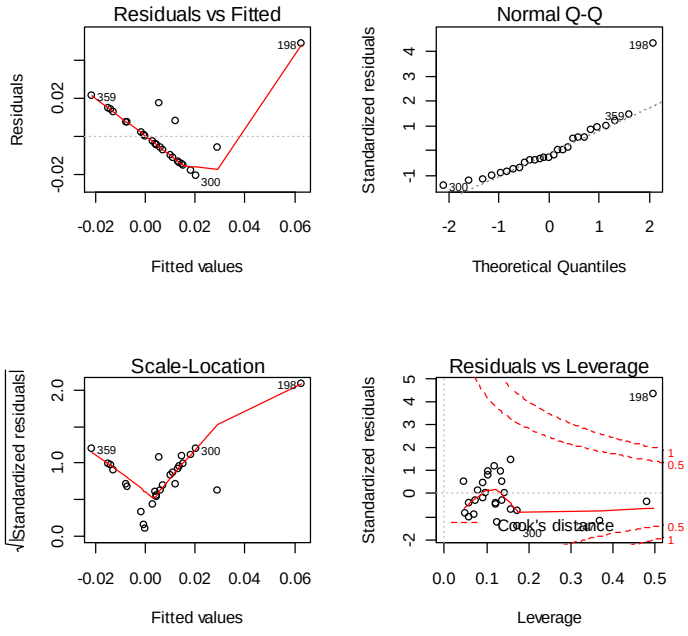
Residual standard error: 0.01598 on 23 degrees of freedom

(530 observations deleted due to missingness)

Multiple R-squared: 0.5405, **Adjusted R-squared: 0.4805**

F-statistic: 9.017 on 3 and 23 DF, **p-value: 0.0003924**

Diagnostic graphs of the candidate



Response y2

lm(formula = log (y2 +1) ~ Pt + Bp2 + SC - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.036879	-0.014950	0.001561	0.009215	0.068559

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Pt	-2.723e-05	3.585e-05	-0.760	0.452726
Bp2	5.880e-02	1.599e-02	3.677	0.000808 ***
SC1	1.472e-02	1.720e-02	0.856	0.398011
SC2	-2.650e-03	9.398e-03	-0.282	0.779688
SC3	-2.779e-03	9.602e-03	-0.289	0.774020
SC4	-2.423e-02	1.614e-02	-1.501	0.142475
SC5	6.332e-03	2.677e-02	0.236	0.814467

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

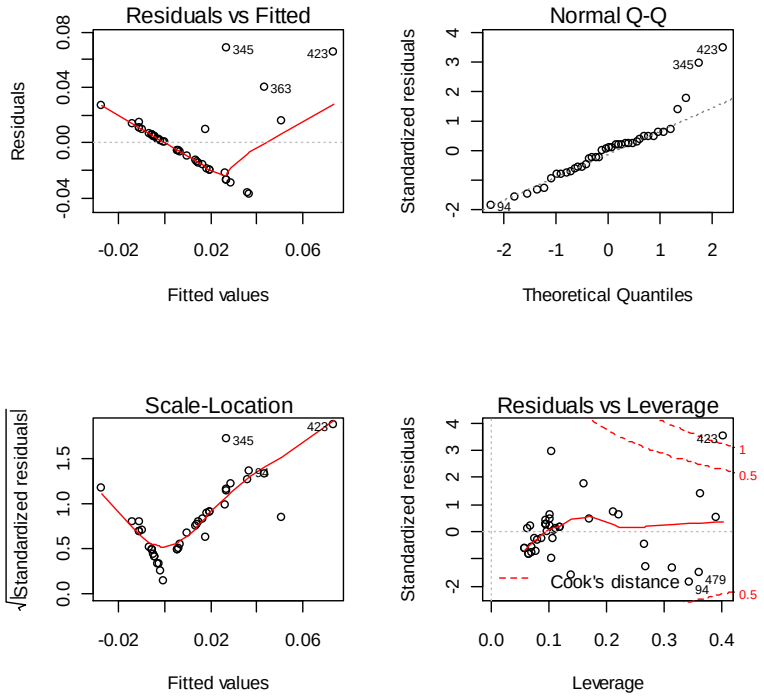
Residual standard error: 0.02443 on 34 degrees of freedom

(516 observations deleted due to missingness)

Multiple R-squared: 0.4998, **Adjusted R-squared: 0.3968**

F-statistic: 4.852 on 7 and 34 DF, **p-value: 0.0007145**

Diagnostic graphs of the candidate



Response y3

lm(formula = log (y3+1) ~ Pt + S3 + SC - 1, data = mydata)

Residuals:				
Min	**1Q**	**Median**	**3Q**	**Max**
-0.071592	-0.020908	-0.009434	0.004589	0.206594

Coefficients:

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Pt	-5.888e-05	1.741e-05	-3.383	0.000821 ***
S3	3.426e-02	7.668e-03	4.468	1.16e-05 ***
SC1	-1.726e-02	1.158e-02	-1.490	0.137333
SC2	-1.527e-02	1.249e-02	-1.222	0.222675
SC3	-2.996e-02	1.344e-02	-2.230	0.026571 *
SC4	-1.195e-02	1.682e-02	-0.710	0.477997
SC5	-3.560e-02	1.990e-02	-1.789	0.074693 .

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

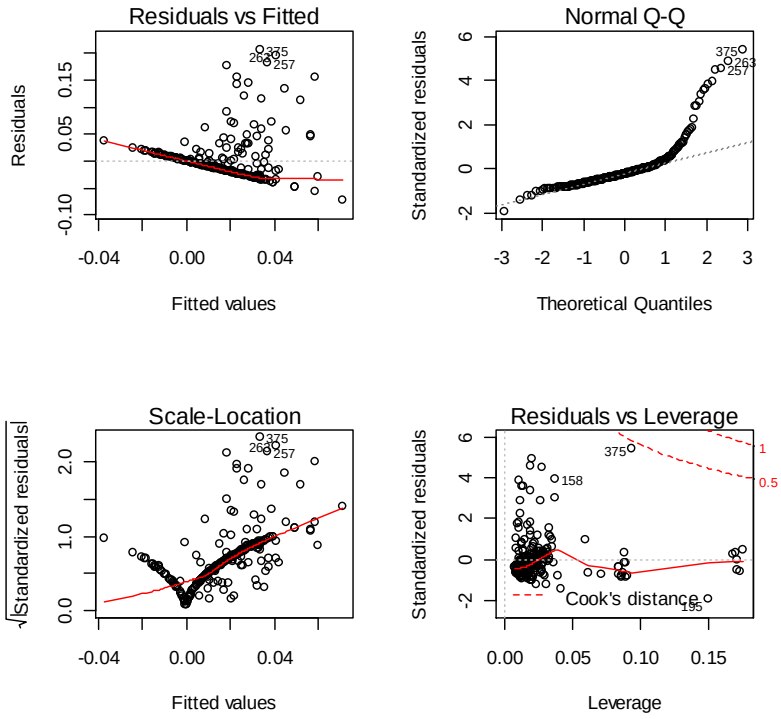
Residual standard error: 0.04033 on 275 degrees of freedom

(275 observations deleted due to missingness)

Multiple R-squared: 0.2536, **Adjusted R-squared: 0.2346**

F-statistic: 13.35 on 7 and 275 DF, **p-value: 8.007e-15**

Diagnostic graphs of the candidate



The selection among the potential candidates was based on the following criteria: R^2, p-value and diagnostic plots of each candidate model.